Individual Differences in Learning, Personality, and Social Success in Brown Capuchin Monkeys (*Sapajus sp.)*

A thesis submitted for the degree of
Doctor of Philosophy

By

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2014

This dissertation is the result of my own work and includes nothing which is the outcome of work done in collaboration except where explicitly indicated within the text.

No part of this dissertation has been or is to be submitted for a degree or diploma or other qualification at any other university.

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F. Blake Morton

Summary

This thesis examines the relationship between individual differences in learning, personality, and social success in two groups of brown capuchin monkeys (*Sapajus sp.*) housed at the "Living Links Centre for Human Evolution" at Edinburgh Zoo, UK. Being able to learn quickly and efficiently likely helps primates achieve social success (defined here in terms of centrality within a social network), such as acquiring knowledge of others or learning social skills. Therefore, individuals that are better at learning were predicted to have greater social success than other group members. This prediction, however, contrasts with hypotheses generated from two other disciplines at the individual level: 1) the study of behavioural innovation, and 2) the study of individual differences, i.e. "personality". In terms of behavioural innovation, better learners should have *less* social success than other group members because they are expected to rely more on problem-solving, rather than physical combativeness or status, to gain access to socioecological resources. In terms of personality, learning should have little or no *direct* relationship with social success because other individual differences, like sociability and fearfulness, should mediate primates' social decision making. This thesis investigates each of these hypotheses.

Personality was assessed in 127 capuchins from 7 international sites using the Hominoid Personality Questionnaire, and then validated at Living Links (LL) using behavioural codings; this was the first-ever description of personality structure in brown capuchins. Brown capuchins have five personality dimensions: Assertiveness, Openness, Sociability, Neuroticism, and Attentiveness. Ratings were consistent across observers, and predicted relevant behaviours among the LL capuchins over a year later (e.g. scores on Sociability predicted time spent in close

proximity to others). “Social success” in the LL capuchins was assessed in terms of centrality in spatial proximity networks. Individual scores on social network centrality were significantly correlated with scores derived from a Principal Components Analysis of eight affiliative and agonistic behaviours among the LL capuchins, indicating that spatial proximity is a reliable measure of the quality of subjects’ social embeddedness within their groups. Social rank and two personality traits (Assertiveness and Sociability) were positively related to network centrality, while another personality trait (Neuroticism) was negatively related to centrality. Sociability was a significant predictor of network centrality even after controlling for social rank and the other personality traits, highlighting the importance of this personality trait in shaping the social success of capuchins beyond that of basic social rules (e.g. kinship, sex, and rank).

Individual learning was assessed in the LL capuchins by administering two operant tasks to subjects under conditions of free choice participation. In Task 1, thirteen monkeys participated, and eight individuals met learning criteria (i.e. >80% trials correct over 3 consecutive sessions). In Task 2, fifteen monkeys participated, and five individuals met learning criteria; the monkeys that learned this second task were also among those individuals that learned Task 1. For monkeys that regularly participated in both tasks (i.e. >50% of sessions), their average performances (i.e. % trials correct) were significantly correlated with individual scores on Assertiveness, but not the other four personality traits, or individual differences in attention span during testing, the percent of sessions subjects participated during testing, the amount of scrounging events subjects directed towards others within their social group, or the percent of observation time subjects spent feeding within their main indoor/outdoor enclosures. In terms of social success, relatively better learners had lower social rank and network centrality compared to relatively poor learners. Also, compared to poorer learners, better learners were generally less likely to direct affiliative acts (e.g. grooming, food sharing, coalitionary support) to other group members. Controlling for Assertiveness (i.e. the only variable related to individual differences in subjects' average learning performance), individual differences in learning performance were no longer significantly related to social rank, network centrality, or the amount of affiliative acts subjects initiated with others. Collectively, such findings contrast the hypothesis that better learners should (concurrently) be more socially successful than poorer learners, and instead are more reflective of hypotheses pertaining to behavioural innovation and/or the study of individual differences. Social rank and certain traits of personality (Assertiveness, Openness, Neuroticism, and Sociability) appear to interact with capuchins' patterns of social interaction, and one personality trait (Assertiveness) may mediate how individual differences in learning are associated with differences in social success.

Acknowledgements

I acknowledge all those that directly or indirectly helped me during this PhD. In particular, I would like to thank Prof. Phyllis Lee (my primary supervisor) and Prof. Hannah Buchanan-Smith (my secondary supervisor) for giving me the opportunity to work with them, and for offering their immeasurable expertise, patience, and support throughout all stages of planning, data collection, and writing for this thesis.

I would also like to thank Prof. Andrew Whiten, Director of Living Links, for permission to work at this facility, and all of the staff and students who kindly gave advice and support during data collection – particularly, Nicolas Cladiere, Mark Bowler, Emily Messer, Alison Dowling, Sophie Pearson, Debbie Bryson, Amanda Dennis, Gillian de Felice, and Roslin Talbot.

I would like to thank all of the people involved in the personality study, particularly the many raters who took time to complete the questionnaires, and my co-authors Sarah F. Brosnan, Annika Paukner, Bernard Thierry, Frans B. M. de Waal, Jennifer Essler, Jane Widness, and Alexander Weiss. Alexander Weiss played a critical role in helping to orchestrate this study for which I am very grateful.

I would like to thank all of my fellow PhD students for their friendship and advice, particularly Lizzie Webber, Emma Scott-Smith, Catherine MacLeod, Mala Narayana, Adam Milligan, Vanessa Wilson, Michelle Klailova, Vicki Fishlock, Johanna Simpson, and Eoin O’Sullivan. I thank the members of the Behaviour and Evolution Research Group, particularly Jim Anderson, Christine Caldwell, and Sarah J. Vick, for their help and advice during the early planning stages of my research. I am very grateful to Catriona Bruce and Stephen Stewart for their endless computer and video camera technical support, and to the staff in the main office of the Psychology department at the University of Stirling for their administrative assistance, particularly Stella Turner, Roswitha Lucht, Linda Cullen, and Nicola Hunt.

Special thanks go to Alexander Weiss for many discussions on the statistical content of Chapter 3 and 4 of this thesis, and for running several statistical analyses for these chapters. I also thank Eoin O'Sullivan for coding monkeys' attention span scores used for the inter-observer reliability tests in Chapter 3. Alain Macri and Russel Demptser graciously provided the cubicle diagrams used in Chapter 2 to illustrate my learning tasks, Mark Bowler provided the photo used on the cover page of Chapter 7 as well as Figure 4, and Emily Messer provided the photo in Figure 3.

I would like to thank my examiners, Drs. Nicola Koyama and Sarah J. Vick, for having a pleasurable discussion with me about my research, and for providing all of their useful suggestions on how to improve the contents of this work. I also thank Alex Weiss for helpful comments on Chapters 1, 4, and 8, and Andrew Whiten for his comments on Chapter 8.

Most important of all, I would particularly like to thank my family for their endless love and support – I would not be where I am today without you!

I am also very grateful to the Primate Society of Great Britain and the University of Stirling for awarding grants to fund my research; thank you for taking interest in my work!

Finally, although they can't read this, I would like to thank the capuchins at Living Links, those dear little gremlins, for teaching me more about the animal mind than any text book could ever have achieved.

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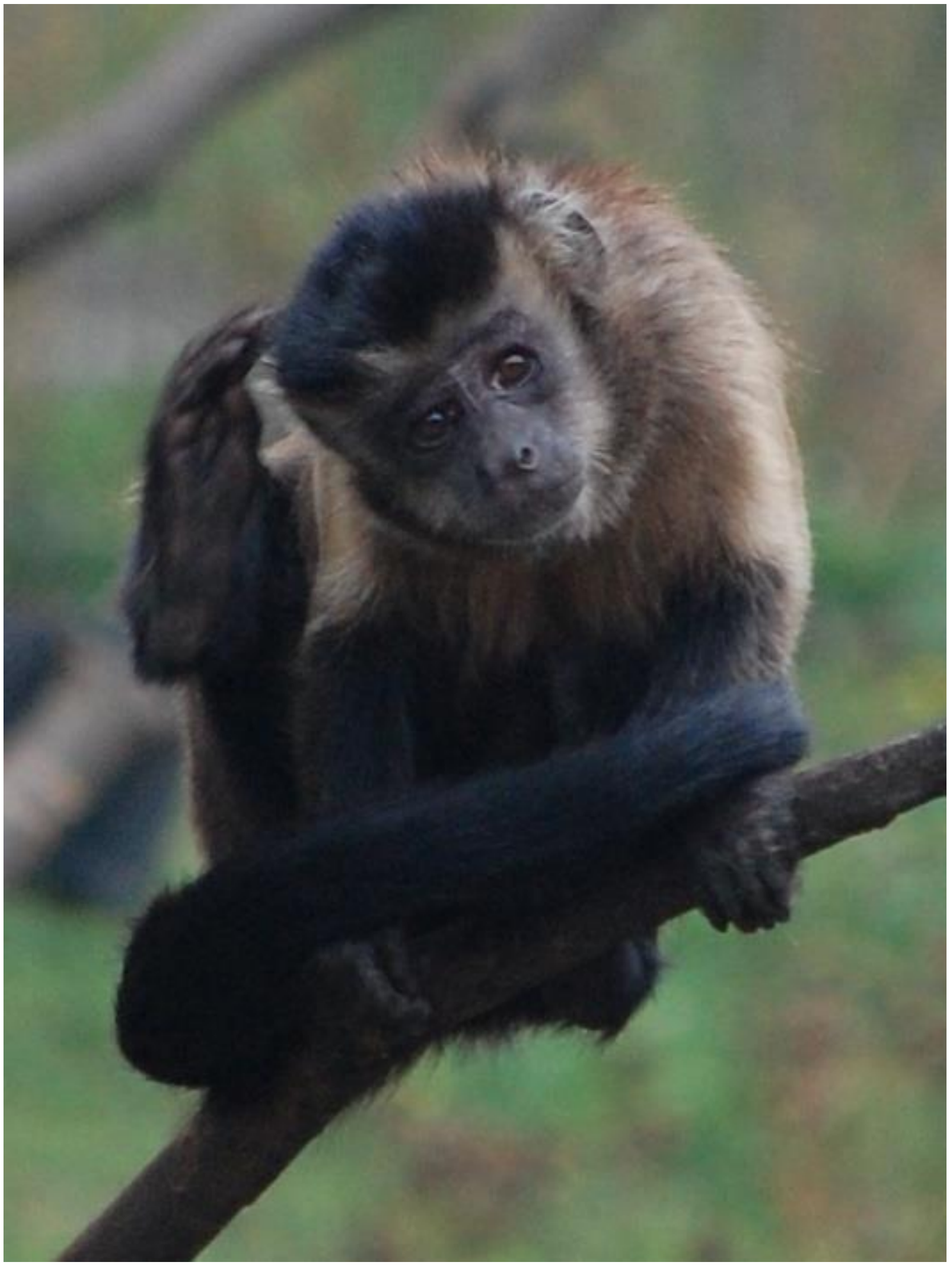


Photograph 1

CHAPTER 1

General Introduction and Aims

1.1. General Introduction

Primates are renowned for their behavioural flexibility and cognitive and learning skills (i.e. “intelligence”, Neisser et al. 1996). Primates typically outperform most animals on a range of tasks, such as reversal learning, tool use, delayed gratification, and social inference (Tomasello and Call 1997). Compared to many taxa, primates also have one of the largest brain sizes relative to their body size, including a particularly large neocortex – a region of the brain critical to sensory perception, information processing, and rational decision-making (Lui et al. 2011). Such observations raise many questions regarding the adaptive function of primate intelligence, particularly with regards to what selective pressures drive its evolution (e.g. Byrne and Whiten 1988).

According to the Social Intelligence Hypothesis (SIH), primates’ intelligence evolved in order to manage the intensity and diversity of their social environment (Byrne and Whiten 1988; Dunbar 1998). In particular, as group-living became more socially demanding, the SIH proposes that primates increasingly relied on sophisticated strategies, such as deception, cooperation, and exploitation of others’ knowledge, to compete for greater social success (Humphrey 1976; Byrne and Whiten 1988).

Relationships vary between interactants in terms of content, quality, and temporal patterning (Hinde 1976). Frequent affiliative interactions over time can result in higher-quality relationships, which in turn can affect an individual’s behaviour and fitness in a variety of ways. For example, individuals with higher-quality relationships may show reduced behavioural and/or physiological responses to stress (Castles et al. 1999; Heinrichs and Domes 2008; Majolo et al. 2009). Individuals with higher-quality relationships may also have greater opportunities for mating (Schulke et al. 2010; Massen et al. 2012; Langergraber et al. 2013), higher rates of agonistic support (Koyama et al. 2006; Schino 2007; Fraser and Bugnyar 2010), priority access to food (Janson 1990), better protection from infanticide (van Schaik and Kappeler, 1997; Ebensperger 1998; Palombit 2000; Borries et al. 2010), and/or experience lower levels of conflict (Fraser and Bugnyar 2010; Rebeccini et al. 2011; Tiddi et al. 2011). For juveniles, the formation of social relationships can be particularly important in terms of integrating themselves within their group (Hinde and Spencer-Booth 1967). Finally, individuals with higher-quality relationships can have greater longevity and increased offspring survivorship (Silk et al. 2003, 2010). Relationships are thus one direct measure of “social success”. Therefore, based on the SIH, having the mental capacity to achieve greater social success may have evolved in primates because it was an important strategy for improving one’s individual and reproductive fitness (e.g. Pawlowski et al. 1998).

The basis for the SIH comes from observations on primates’ seemingly calculative and “political” behaviour towards others (de Waal 1982; Byrne and Whiten 1988). For instance, in white-faced capuchin monkeys (*Cebus capucinus*) individuals that are engaged in a fight will preferentially solicit coalition partners that are more dominant and with whom they share a stronger social bond than their opponent (Perry et al. 2004). In chimpanzees (*Pan troglodytes*), individuals being aggressed by another group member have been observed exaggerating their alarm screams if they are within auditory distance of an ally whose rank and bond with them is higher than with their opponent (Slocombe and Zuberbuhler 2007). Lastly, in many primates, individuals engage in tactical deception to manipulate the behaviour of others, such as using an alarm call outside its normal context in order to distract and steal food from others (Whiten and Byrne 1988; Wheeler 2009).

Experimental studies corroborate what observational studies of primate behaviour suggest; that is, primates are capable of classifying others on the basis of kinship and rank, can recognize third-party social relationships, and (to some extent) are able to discern the attentional states of others (Cheney and Seyfarth 1990; Seyfarth and Cheney 2000; Perry et al. 2004; Wheeler 2009). For instance, playbacks of vocalizations simulating rank reversals (e.g. a subordinate aggressing a dominant) induce longer looking times among baboons (*Papio cynocephalus ursinus)* and vervet monkeys (*Chlorocebus aethiops pygerythrus*) compared to playbacks simulating a normal situation (e.g. a dominant aggressing a subordinate) (Cheney et al. 1995; Borgeaud et al. 2013). In rhesus macaques (*Macaca mulatta*), females respond more often to calls emitted by their paternal half-sisters compared to those given by unrelated females, and this discrimination cannot be explained merely by how familiar test subjects were with each caller (Pfefferle et al. 2014). Lastly, when competing with a human observer to gain access to a food reward, chimpanzees spontaneously approach the food using a route hidden from the observer’s view, suggesting they are sensitive to what the observer can and can not see (Hare et al. 2006).

Further support for the SIH comes from phylogenetic analyses. Across a range of primate species, species differences in relative brain size (a putative measure of intelligence; Deaner et al. 2007) are closely associated with species differences in sociality, such as group size (Dunbar 1989), grooming clique size (Lehmann and Dunbar 2009), and rates of tactical deception (Byrne and Corp 2004). Species that differ in the intensity of their sociality also perform differently on cognitive tasks. For example, highly social ring-tailed lemurs (*Lemur catta*) outperform less social mongoose lemurs (*Eulemur mongoz*) on a task designed to measure their transitive reasoning abilities (which presumably is used to infer third-party social relationships; MacLean et al. 2008).

One interpretation of findings from higher-taxonomic levels is that social complexity among primates selects for intelligence at the individual level. For instance, Humphrey (1976, p. 311) proposed that "if intellectual prowess is correlated with social success, and if social success means high biological fitness, then any heritable trait which increases the ability of an individual to outwit his fellows will soon spread through the gene pool…to increase the general intellectual standing of the species". Therefore, individuals that are more intelligent may achieve greater social success because their mental abilities allow them to do so (Dunbar 1998). In support of this notion, as previously noted, primates use social knowledge to improve their own status within groups. In humans and captive rhesus macaques (*Macaca mullatta*), Powell et al. (2012) and Sallet et al. (2011) found that individuals with larger social networks also have larger relative brain sizes compared to others. Importantly, however, behaving "intelligent" is not the same as *being* intelligent (e.g. Drea and Wallen 1999) since an individual's behaviour is easily influenced by opportunity, physiological state, and motivation (Shettleworth 2009). Thus, observations of socially intelligent behaviour among primates do not provide a reliable measure of individual differences in mental ability *per se*. Moreover, the extent to which brain size is a reliable measure of intelligence, particularly at the individual level, remains highly debated (Healy and Rowe 2007). For these reasons, data on primates' performances on cognitive and learning tasks, which can be administered to individuals under controlled experimental conditions, may provide researchers with a more direct assessment of the relationship between individual differences in intelligence and social success.

Learning is defined in terms of acquiring new or modifying existing knowledge, behaviours, or skills through experience (Shettleworth 2009). The tendency to invent novel solutions to problems (i.e. via asocial learning processes) or to acquire new skills and behaviours by watching others (i.e. via social learning) has undoubtedly played an important role in the evolution of primate intelligence. In a comparative analysis of 116 primate species, Reader and Laland (2002) found that species differences in rates of individual and social learning were both positively associated with species differences in relative brain size. While some authors have proposed that higher-order cognitive abilities may underlie primate social intelligence, others contend that many of these behaviours simply reflect basic associative principles (reviewed in Barrett et al. 2007). For example, primates' sensitivity to eye gaze may reflect meta-cognitive skills (Call and Tomasello 2008), but could also reflect subjects having learned a simple stimulus-reward contingency (e.g. Vick and Anderson 2000). Going further, primates show difficulty in suppressing inappropriate social responses, such as emitting food-related calls to potential scroungers when food has been found (Gros-Louis 2004), which seems counter-intuitive if those species are aware of their "mentalizing" states, and thus have the flexibility to understand the consequences of their actions. Indeed, Chapais (1992) found that when the relatives of certain high-ranking juvenile macaques (*Macaca fuscata*) were removed from their enclosure, the juveniles continued to challenge other group members despite their lack of tactical support, ultimately resulting in their losing their position within the group's social hierarchy. Finally, although primates may have knowledge about relationships between other group members (i.e. third-party relationships), Range and Noë (2005) argue that in at least some species, like sooty mangabeys (*Cercocebus torquatus*), individuals could acquire this knowledge by learning to follow a basic set of rules, thereby rendering the need for higher-order cognition obsolete.

The learning contingencies necessary to achieve social success within primate groups are likely to be complex. Acquiring the skills to deceive others, classifying conspecifics on the basis of kinship and rank, recalling third-party relationships, and gauging whether individuals are likely to cooperate versus defect based on prior interactions all require an efficient capacity to learn and remember (e.g. Byrne 1997; Barrett et al. 2007). Moreover, as previously noted, much of the socially intelligent behaviour seen among primates could be explained through simple associative learning (Barrett et al. 2007). Therefore, based on the SIH, if better learners are "better-equipped" to learn and remember how to solve social challenges through innovative means, like tactical deception, or through generalizing associative principles across contexts, then they might also be more socially successful within their group (Figure 1a). This hypothesis, however, contrasts hypotheses generated from two other disciplines of research at the individual level, including 1) the study of behavioural innovation among animals, and 2) the study of personality (i.e. individual differences in behavioural consistency across time and contexts; Gosling 2001).

Innovation, defined here as having the ability to respond to novel circumstances by using new behaviours (Kummer and Goodall 1985; Lee 1991), is an important component of behavioural plasticity that relies on individual learning skills (Reader and Laland 2003). It has significant links with intelligence, drives the evolution of "cultural" traditions among species, and can increase the breadth of one's ecological niche within the environment (van Schaik and Burkart 2011; Overington et al. 2011). Animals innovate presumably because they need to in order to meet ecological demands (e.g. energy constraints; Moura and Lee 2004; Sanz and

Morgan 2013). According to many behavioural innovation studies, poorer competitors are expected to be better at learning than better competitors as a result of their having to use brains, not brawn or status, to gain access to desirable resources (e.g. food, mates, and social partners). For example, in capuchin monkeys (*Sapajus apella*), Wheeler (2009) reported that lower-ranking individuals developed false alarm calls to distract higher-status group members while they sought access to a contestable food source. Similarly, among chimpanzees (*Pan troglodytes*), incidences of innovation occur more often among lower-ranking than higher-ranking individuals (Reader and Laland 2001). Therefore, in contrast to Hypothesis 1 (Figure 1a), better learners may be less socially successful compared to other members of their group (Figure 1b).

In terms of studies on personality, research suggests that certain personality traits may underlie individual differences in the general decision-making of animals, including their performance on tasks. For example, slow-exploring guppies are often better spatial navigators (Burns and Rodd 2008), less neophobic birds have a tendency to be faster learners (Boogert et al. 2006), and extraverted humans are generally better at mental updating (Campbell et al. 2011). Therefore, individual differences in learning among primates may not be *directly* related to differences in social success, but instead may be mediated by one or more of their personality traits (Figure 1c). This latter hypothesis pertaining to personality is particularly significant because it suggests that the selective pressures on personality may be a key factor underlying the evolution of primate intelligence. Indeed, personality has been linked to several key components to the SIH, particularly variation in social relationships (discussed in Chapters 4 and 5) and brain size and function (De Young et al. 2010; Blatchley and Hopkins 2010; Adelstein et al. 2011). Moreover, bonobos (*Pan paniscus*), for example, perform better on tasks involving ‘theory of mind’, while chimpanzees perform better on tasks involving tool use (Herrmann et al. 2010).

Although such differences in task performance may reflect species differences in cognitive and learning skill, Herrmann et al. (2010) point out that the relatively tolerant and shy personality of bonobos may also be an important contributor.

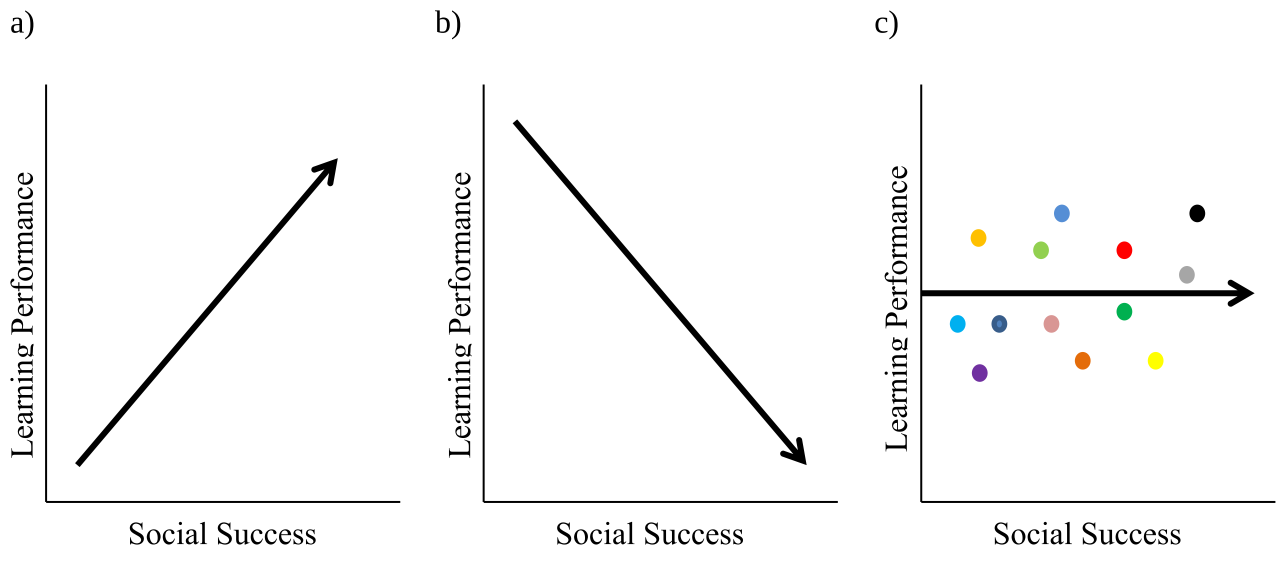


Figure 1. Illustration of the main research hypotheses of this thesis pertaining to the relationship between learning and social success among primates based on a) the Social Intelligence Hypothesis, b) studies of behavioural innovation among animals, c) studies of individual differences in personality. The latter hypothesis predicts no *direct* relationship between learning and social success as this relationship may be mediated through individual differences in personality.

1.2. Thesis Aims

This thesis aims to test each of the hypotheses outlined in Figure 1 within a captive population of brown capuchin monkeys (*Sapajus sp.*), housed at the "Living Links to Human Evolution" Research Centre, Edinburgh Zoo, UK. Capuchins are renowned for their relatively large brains, advanced learning abilities, socially intelligent behaviour, curiosity and innovativeness (e.g. tool use), and complex social organization (see Chapter 2). Moreover, compared to many Old World monkey species (e.g. baboons, vervet monkeys, and rhesus macaques) capuchins are relatively more socially tolerant of conspecifics, including non-kin, and also exhibit lower rates of agonism; as such, they potentially have greater choice compared to many Old World monkey species in terms of their interactions with others. Using strategies to achieve social success within capuchin groups may therefore outweigh the costs of detection (e.g. physical conflict; Drea and Wallen 1999). For these reasons, capuchins are an ideal species for testing the hypotheses of this thesis (see Chapter 2 for further discussion).

This thesis is structured as follows. Chapter 2 provides a general description of the biology of brown capuchin monkeys, including their morphology, taxonomy, life history, diet, sociality, cognitive and learning abilities, and social intelligence. This chapter also provides a general description of the research site and study subjects, as well as the methods of data collection and analysis.

Using questionnaire-based methods, Chapter 3 describes the personality structure (i.e. the number of traits and their characteristics; Morton et al. 2013) of brown capuchins within a large multi-site sample of capuchins. Inter-rater reliabilities were tested, and individual scores were calculated per monkey for each personality trait and validated within the Living Links population using behavioural codings. The personality scores for each monkey at Living Links were used in the remaining chapters where indicated.

Chapter 4 examines the social relationship structure (i.e. the number of components and their characteristics) of the brown capuchins at Living Links using data collected on the affiliative and agonistic interactions of each monkey dyad, and subjecting these data to a principal components analysis (PCA). A PCA was first conducted using Kaiser's criterion and scree plots (i.e. two methods that are unreliable and highly subjective, yet commonly used by researchers to determine how many components to extract from a PCA; Zwick and Velicer 1986). These results were then compared to a PCA in which parallel analysis was used (i.e. a more robust method of component extraction; Zwick and Velicer 1986). This chapter highlights the importance of making careful decisions regarding which methods to use when extracting components from a PCA, and how such decisions can lead to different conclusions regarding comparisons of social relationship structure between species.

Chapter 5 examines what factors affect differences in the social relationship quality of capuchins at Living Links. Relationship quality scores were calculated for each dyad using analyses from Chapter 4, and each dyad's scores were correlated with similarities in each social partner's social rank, age, sex, kinship, and personality. This chapter aims to determine the extent to which similarities in partners' personality explains dyadic variation in the quality of their social relationship beyond that explained by basic social rules (i.e. rank, age, sex, and kinship).

Chapter 6 examines what factors (personality, age, sex, kinship, rank) are related to individual differences in the social network position of capuchins at Living Links using data collected on each subjects' spatial proximities with others in their group. In light of recent advances in the use of social network analysis to study animal behaviour (e.g. Croft et al. 2008; Whitehead 2008), task performance was compared with the eigenvector centrality (hereafter "centrality") of each subject within its social network. Centrality takes into account both the number and intensity of each subject's social interactions relative to everyone else within the network (Whitehead 2008), and therefore provides a measure of social success as defined in this thesis. Social network position was calculated for each monkey, and correlated with their mean relationship quality scores with each group member (using data from Chapter 4); the purpose of this analysis was to determine whether the structure of these spatial networks were representative of subjects' affiliative and agonistic relationships. This chapter also examines the extent to which personality explains individual differences in network position beyond that explained by basic social rules (i.e. rank, age, sex, and kinship).

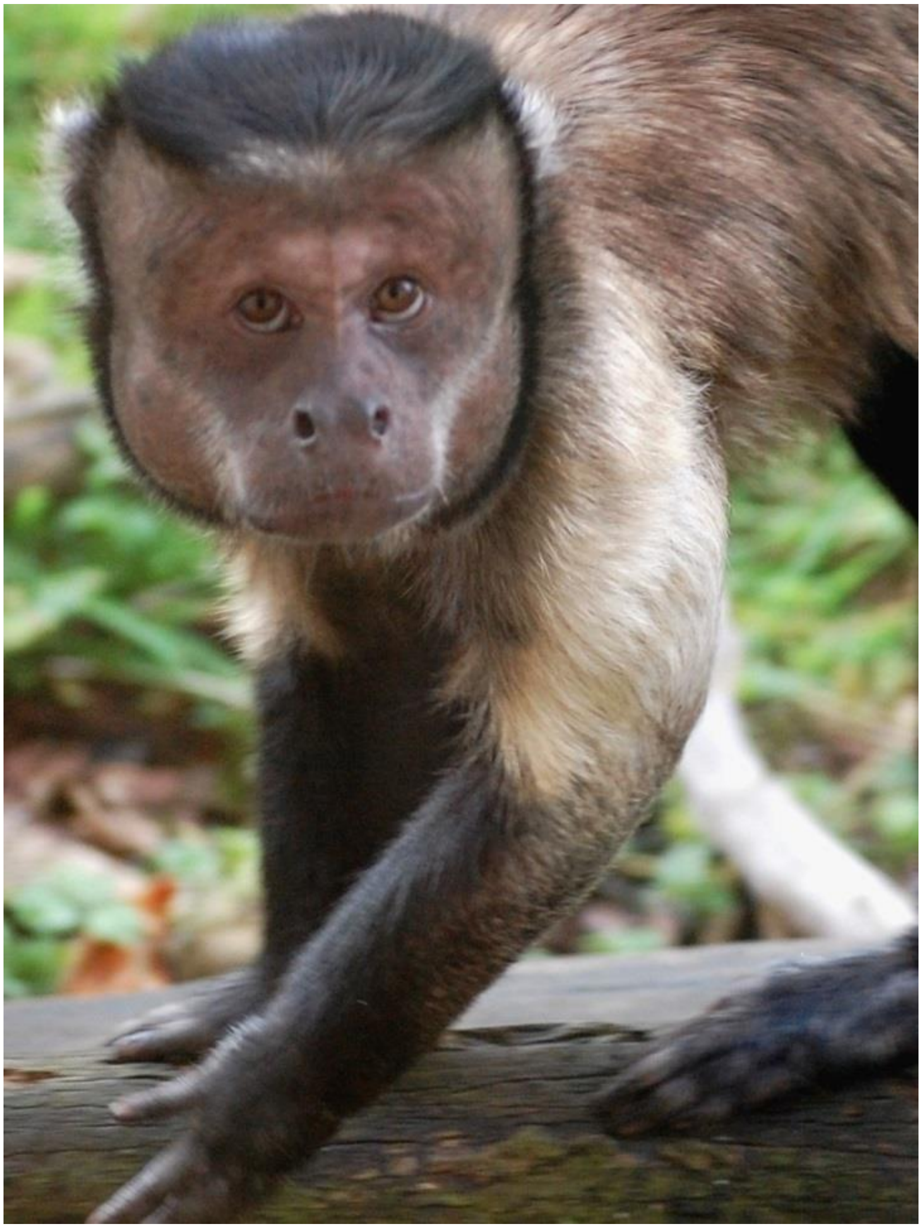
Chapter 7 assesses individual differences in the learning performance of the Living Links capuchins using two operant tasks. This chapter also investigates what factors might underlie variation in subjects' average performance on tasks, including individual differences in attention span during testing, average participation on tasks, personality, time spent feeding and scrounging within the group's main indoor/outdoor enclosure, and age.

Chapter 8 investigates among the Living Links capuchins the relationship between individual differences in their learning performance and social success (defined here in terms of social network position). In addition, differences in subjects' learning performance were correlated with differences in the number/frequency of affiliative acts (i.e. grooming, food sharing, and coalitionary support) they directed towards others within their group. To facilitate interpretations of these results, learning performance was compared with individual differences in subjects' age, sex, kinship, and social rank.

Finally, Chapter 9 provides a general discussion of the results found in the previous chapters, and examines the core hypotheses of this thesis (Figure 1).

CHAPTER 2

General Methodology



Photograph 2

CHAPTER 2

General Methodology

2.1. Introduction

The following chapter provides an overview of the biology of brown capuchin monkeys. A general description of the study site, subjects, and methods of data collection and analysis is also presented.

2.2. Brown Capuchin Biology

2.2.1. Morphology and Taxonomy

Brown capuchins are a New World monkey, known for their distinctive dark “tuft” of pelage on the top of their head. Adults usually weight somewhere between 2-4kg, with adult males being heavier and larger than females, and can range between 32-57 centimetres in height from head to body (Fragaszy et al. 2004). Classified as quadrupeds, brown capuchins have semi-opposable thumbs and a semi-prehensile tail, the latter being used primarily for locomotion and postural support (Fragaszy et al. 2004).

Brown capuchins were formerly classified as *Cebus apella*. Recently, however, Alfaro et al. (2012) proposed that brown capuchins should be reclassified under a separate genus, *Sapajus*, in light of differences in their morphology, behaviour, and geographical distribution compared to other species of Cebus (e.g. white-faced capuchins, *Cebus capucinus*). In particular, compared to *Cebus*, which are relatively gracile, brown capuchins have a more robust jaw and thicker dental enamel, which they use to open hard foods (e.g. palm nuts). Moreover, unlike *Cebus,* brown capuchins are the most widely distributed New World primate, ranging throughout southern

Columbia, the eastern regions of the Andes, much of the Amazon basin, southern Brazil, Paraguay, and northern Argentina (Fragaszy et al. 2004). In terms of diet, brown capuchins are omnivorous, have a more flexible seasonal diet compared to *Cebus*, and have the capacity to manipulate their environment (e.g. tool use; Visalberghi et al. 1995). It has been proposed that such dietary and behavioural habits allow brown capuchins to occupy a much wider geographic range compared to other capuchin species (Fragaszy et al. 2004).

In light of their recent taxonomic reclassification, this thesis uses the term *Sapajus* to reference brown capuchin monkeys.

2.2.2. Social Behaviour

Most breeding populations of capuchins in captivity reflect patterns of sociality comparable to those in the wild. As with wild capuchins, individuals in captivity exhibit a dominance hierarchy among both sexes, with one male that is dominant over all other group members (i.e. “alpha”), and female mate choice is biased towards this alpha male (Janson, 1984; Alfaro 2005). Like wild capuchins, captive capuchins also engage in affiliative acts like grooming, food sharing, and coalitionary support in order to form and maintain relationships with others in their group (Parr et al. 1997; Ferreira et al. 2006; Schino et al. 2009; Hattori et al. 2012).

Capuchins are unusual among New World primates in that they are primarily male-dispersing (Strier 1999); males eventually leave their natal group around the time sexual maturity is reached in order to join another group. As with most animals, natal dispersal likely serves as a way to avoid mating competition (Fragaszy et al. 2004; Jack and Fedigan, 2004). The earliest age at which a male emigrates from his natal group is around 6 years of age (Fragaszy et al. 2004).

Although female capuchins may also leave their natal groups, this is observed less frequently than males (Fragaszy et al. 2004). Because females typically remain within their natal group, capuchins are generally regarded as being female-bonded whereby females form strong social relationships with other females in their group (Fragaszy et al. 2004).

Brown capuchin groups generally have twenty group members or fewer, and contain one to several adult males and females (Izawa 1980; Defler 1982). With the exception of newborn infants and young males (who typically emigrate from their natal group), group membership is generally stable over time (Janson 1990).

Both male and female rank hierarchies are associated with age, with older capuchins typically being more dominant over younger individuals (Fragaszy et al. 2004). Higher-status capuchins are typically the most socially active members of their group; the alpha male in particular plays an important role in group activity (Izawa 1980; Janson 1990; Tiddi et al. 2011). Although males are usually dominant over females, the alpha female often ranks immediately below the alpha male and is dominant over other adult males within the group (Fragaszy et al. 2004). Subordinates can counteract dominants by forming coalitions with each other (Ferreira et al. 2006). Changes in alpha status are rarely reported with the exception of the alpha male, who may lose his position to the beta male as a result of periods of group instability (Moura 1999).

Active avoidance of dominants by non-tolerated subordinates appears to be the primary determinant of capuchins' spatial positioning within the group; dominant individuals and infants are found more in the centre of the group, while subordinates are found towards the periphery (Janson 1990). Like most group-living animals, a capuchin's position within their group can have important fitness-related consequences, such as foraging success and vulnerability to predators (Janson 1990; Fragaszy et al. 2004).

Unlike most Old World primates (e.g. rhesus macaques, vervet monkeys [*Chlorocebus spp.*], baboons [*Papio spp.*]), capuchins appear to be relatively more tolerant of conspecifics including non-kin (Cooper et al. 2001). For example, alpha males may allow infants and mothers to co-feed at contestable food sources (Fragaszy et al. 2004). Most group members will also aid infants regardless of kinship, such as transporting them across large gaps in the canopy (Fragaszy et al. 2004). Finally, females sometimes solicit and copulate with subordinate adult males in full view of the dominant male without his intervention (Phillips et al. 1994). Aggression among group members is also generally less frequent compared to Old World species; however, females tend to engage in more conflict than males (Fragaszy et al. 2004).

Grooming is one of the most common forms of affiliative contact among capuchins (Parr et al. 1997; Schino et al. 2009; Tiddi et al. 2011; Tiddi et al. 2012). Higher-status individuals groom subordinates as a form of appeasement (e.g. Parr et al. 1997). Adult females often direct their grooming to other females (especially those with new infants; Tiddi et al. 2010); the second most common form of grooming occurs between adult females and adult males (Fragaszy et al. 2004). Parr et al. (1997) found that adjacently ranked individuals are more likely to groom each other. The results of rank-direction grooming among capuchins are thus far mixed, with some studies showing that capuchins groom up the hierarchy (e.g. Tiddi et al. 2012), while other studies reporting that capuchins grown down the hierarchy (e.g. Parr et al. 1997).

Capuchins both in the wild and captivity structure their social relations loosely around multi-generation matrilines (Fragaszy 2004). Welker et al. (1990) reported that matrilines formed the basis of social relationships within their study population. However, kinship does not always predict how capuchins choose to act affiliatively within some populations (e.g. Ferreira et al. 2006; discussed further in Chapters 5 and 6).

2.2.3. Life History and Reproduction

In general, capuchins of less than one year of age are classified as infants, capuchins between 1 and 3 years of age are classified as juveniles, and capuchins between 3 and 4 years of age are classified as sub-adults (Fragaszy et al. 2004). Characteristics of each age group are given in Table 1. Both male and female capuchins reach sexual maturity between four and five years of age (Fragaszy et al. 2004). In captivity, capuchins live up to 40-45 years of age, making them one of the longest-living species of primate (Fragaszy et al. 2004).

Table 1. Age-sex Classifications for Brown Capuchin Monkeys.

Age-sex Classification	**Definition***
Adult male	>4 years old, broad "square-shaped" face and pronounced jaw line.
Adult female	>4 years old, tufted hair on either side of the head's crown.
Sub-adult	Between 3 and 4 years old, approaching sexual maturity.
Juvenile	Between 1 and 3 years old; spend much of their time playing and closely affiliated with their mother.
Infant	<1 year old, still strongly dependent on mother.

*following Fragaszy et al. (2004)

The capuchin mating system is usually classified as multi-male/multi-female, although single-male groups have been reported (Fragaszy et al. 2004). Mate choice in females is biased towards the alpha male of their group, and as such, females devote most of their solicitations and copulatory acts towards the alpha male (Janson 1984; Alfaro 2005). In cases of group instability, however, Janson (1998) has observed “extreme female mating promiscuity” among all adult males within the group. Perhaps the most conspicuous way that a female signals that she is ovulatory is through receptive behaviour: females become skittish, with consistent grimacing and characteristic vocalizations resembling a whistle or a whine (Janson 1984; Fragaszy et al. 2004). During the first several days of peak receptivity, the female will continuously approach and solicit the alpha male (Janson 1984; Carosi et al. 2005; Fragaszy et al. 2004). Initially, the alpha male responds indifferently to the female's advances, but after several days he becomes more responsive and copulates with her (Janson 1984; Carosi et al. 2005). The receptive phase of females lasts from one to eight days, but typically no more than five days (Janson 1984; Phillips et al. 1994). Cycling is not seasonal; the menstrual cycle in captivity averages 20.8 days (Nagle and Denari 1983). Average gestation in captivity is 153 days but can range anywhere from 149 to 158 days (Wright and Bush 1977). Although females experience longer inter-birth intervals as they age, they do not undergo menopause (Fragaszy et al. 2004).

2.2.4. Learning and Cognitive Task Performance

Brown capuchins have one of the largest brain sizes relative to their body size compared to other monkey species (Barton 1999). They have a particularly well-developed cerebral cortex, thalamus, and cerebellum (Fragaszy et al. 2004); the latter structure, the cerebellum, is most notable for being the site where learning takes place (discussed in Chapter 7). Based on their performance on learning and cognitive tasks, capuchins are considered one of the most intelligent New World monkey species (e.g. Deaner et al. 2006). For this reason, they are often used in comparative studies of learning and cognition (Deaner et al. 2006; Amici et al. 2008).

Capuchins, like most primates, must find food in the wild, and experimental evidence suggests that these animals remember the spatial locations of food resources within their home ranges (i.e. "spatial memory"; Janson and Di Bitetti 1997; Janson 1998). Capuchins also engage in tool use both in the wild and captivity, and are one of the few examples of a wild primate using tools to solve foraging tasks other than great apes (Visalberghi et al. 1995; Moura and Lee 2004). Capuchins have a propensity to explore and manipulate their environment which likely facilitates their tool-using performance. For example, capuchins spontaneously perform object-object and object-surface combinations both in the wild and in captivity (Fragaszy and Adams-Curtis 1991; Visalberghi, 1988; Byrne and Suomi 1996), and spontaneously gather information about tool quality (e.g. tool rigidity; Manrique et al. 2011). Studies of rhesus macaques have shown that when individuals are exposed to a broad range of social and physical contingencies, they exhibit greater cognitive and social performance abilities compared to individuals with poorer enrichment (Capitanio and Mason 2000).Thus, the innate curiosity and motivation to explore novel environments likely facilitates capuchins' ability to solve tasks in general (Morton et al. 2013).

In the wild, capuchins use stones to crack open nuts, and young capuchins often watch this process from more experienced individuals (Moura and Lee 2004; Ottoni et al. 2005). Such observations have lead many researchers to study the social learning abilities of capuchins (reviewed in Perry 2011), with some studies reporting that capuchins' ability to learn through observation is qualitatively similar to that of chimpanzees and humans (e.g. learning from others' mistakes; Kuroshima et al. 2008). In addition to social learning, capuchins also possess advanced asocial learning abilities. For example, capuchins have been trained to use touch-screen computers to perform matching-to-sample tasks such as same/different concepts, providing some of the first evidence of analogical reasoning in a New World monkey (e.g. Truppa et al. 2011). Studies have also revealed that capuchins are capable of sorting objects according to various shapes and sizes, which indicates that they incorporate various elements into their working memory (e.g. which objects have been chosen already),while simultaneously remembering which category they are presently sorting (McGonigle and Chalmers 2001; McGonigle et al. 2003). Capuchins also appear capable of learning to use tokens as symbols to flexibly combine quantities and maximize their pay-offs for greater rewards (e.g. Addessi et al. 2007), and are able to control their actions to let lesser rewards pass them by in order to wait for a better reward in the future (Bramlett et al. 2012).

Capuchins' ability to perform well on concept-learning tasks suggests they have the capacity to learn rules (e.g. "choose the stimulus that matches the sample", or "do not choose the stimulus that is different from the sample"; D'Amato and Salmon, 1984; D'Amato et al. 1985, 1986; Wright and Katz 2006). There is evidence to suggest that capuchins can generalize these principles across contexts, thereby enabling them to solve novel tasks faster (e.g. Barros et al. 2002; Poti and Saporiti 2010; Fujita et al. 2011). Other studies, however, suggest capuchins fall within a gray area between associative learners and rule learners (Rumbaugh 1970, 1997; D'Amato and Colombo 1989; De Lillo and Visalberghi 1994; Beran et al. 2008). For instance, in some studies of capuchin tool use, capuchins appear to learn a cause-effect relationship between their actions and outcomes of those actions (Schino et al. 1990), whereas in other studies capuchins failed to learn causal relationships (Visalberghi and Trinca 1989; Visalberghi and Limongelli 1994; Visalberghi et al. 1995). Methodological differences and/or individual differences in personality may underlie some of these mixed results (e.g. De Lillo and Visalberghi 1994; Truppa et al. 2010; Morton et al. 2013).

2.2.5. Social Intelligence

It is clear from behavioural and experimental studies that capuchins acquire and use knowledge about others (i.e. they have "social intelligence"; Byrne and Whiten 1988). For instance, among wild capuchins, potential tool users watch those individuals that are more proficient at using stones to crack nuts (Ottoni et al. 2005; Moura and Lee 2010). In captivity, Falcone et al. (2012) reported that capuchins can monitor and assess the goal of a human experimenter, and use this information to coordinate their own actions to solve a cooperative task. Kuroshima et al. (2008) also found that capuchins are able to capitalize on a partner's failure to solve a puzzle box by trying alternative solutions to open it. In terms of reciprocity, capuchins are more likely to share food with individuals with whom they share a stronger affiliative bond (Sabbatini et al. 2012) and are also more likely to tolerate individuals at feeding sites who groom them most (Tiddi et al. 2011).

Of notable value to social intelligence, studies show that capuchins can anticipate future responses and retain and implement those responses when appropriate (Beran et al. 2012). Additionally, capuchins may have "memory awareness" (i.e. the ability to assess when sufficient information is available to solve a task; Hampton et al. 2004), which may facilitate their ability to gather information about social situations when ignorant and then acting immediately when informed.

Inferring others' attentional states, e.g. through eye gaze and head direction, is an important component to social intelligence because, for example, it affords individuals the opportunity to engage in deceptive acts to gain access to desirable resources (discussed below). Vick and Anderson (2000) found that capuchins are able to use the eye gaze of experimenters as a discriminative cue to locate hidden food. Also, Hattori et al. (2010) reported that capuchins are more likely to reach out for food placed in an experimenter's hand when the experimenter had their eyes open versus closed, suggesting that subjects were sensitive to the experimenter's attentional state before requesting food.

While there are numerous reports of tactical deception among wild great apes and Old World monkeys, very few such reports have been made on wild capuchins (Byrne 1995). It remains unclear, however, whether the lack of reports for capuchins is merely due to a lack of published material, or capuchins' lack of motivation to "spontaneously" engage in deceptive strategies under certain contexts (e.g. Fujita et al. 2002). Nevertheless, studies in the wild and captivity demonstrate that tactical deception falls within the capacity of capuchins. Amici et al. (2012) reported that subordinate capuchins were capable of withholding information about a task when more dominant individuals were nearby, and would only approach and solve the task when they were alone. Mitchell and Anderson (1997) found that capuchins were similar to four year old children and human-socialized chimpanzees in their ability to deceive others by indicating (accurately or falsely) the location of hidden food to others. In the wild, Wheeler (2009) experimentally demonstrated that subordinate capuchins were more likely to use predator alarm calls during times of high feeding competition, suggesting that they used these calls in a functionally deceptive manner to gain access to food.

2.3. Study Site and Subjects

The main site for this study was the "Living Links to Human Evolution" Research Centre (LL), which was located within the Royal Zoological Society of Scotland (RZSS), Edinburgh Zoo, UK (MacDonald and Whiten 2011). Monkeys from five additional sites were participants in a study of brown capuchin personality, and the details of those sites can be found in Chapter 3.

2.3.1. Background on Living Links

LL was opened in May 2008 for research and public visitation, and was designed as a facility that combined research with public engagement with science using a variety of methods like visual and interactive displays (e.g. posters, video documentaries, and touch-screen games illustrating research conducted at LL) as well as public-access areas where onlookers can view research in action (e.g. on-going outdoor behavioural studies, or non-invasive experiments conducted within research cubicles; MacDonald and Whiten 2011). Since 2008, numerous undergraduate and graduate studies have been conducted on the primates housed at LL, on topics such as asocial learning and personality (this study), social learning (Messer 2014), facial attractiveness (Griffey 2011), token exchange (Dufour et al. in prep.), photo perception (Morton et al. under review), housing enrichment (Leonardi et al. 2010), the effects of relocation on social networks (Dufour et al. 2011), and the effects of an impending change in alpha-male on social networks (Loudon 2012).

LL operates on the highest ethical standards for research (e.g. following guidelines published by the Association for the Study of Animal Behaviour; ASAB 2012). There is a team of seven staff members who are responsible for the daily care and husbandry of the monkeys; this team works at LL continuously throughout the year to ensure high welfare standards.

2.3.2. Study Subjects and Housing Conditions

LL houses two breeding groups of brown capuchin monkeys, each of which live within identically designed, but mutually exclusive, 189 m^3 indoor enclosures with natural light and near-permanent access to a 900 m^2 outdoor enclosure containing trees and other vegetation, providing ample opportunity to engage in natural behaviours. The indoor/outdoor enclosures for each group are mirror images of each other, with public-access viewing platforms on either side of these enclosures (Figure 2). Each group shares its indoor/outdoor enclosure with a group of common squirrel monkeys (*Saimiri sciureus*); however, the capuchins do not have access to the squirrel monkeys' indoor enclosure.

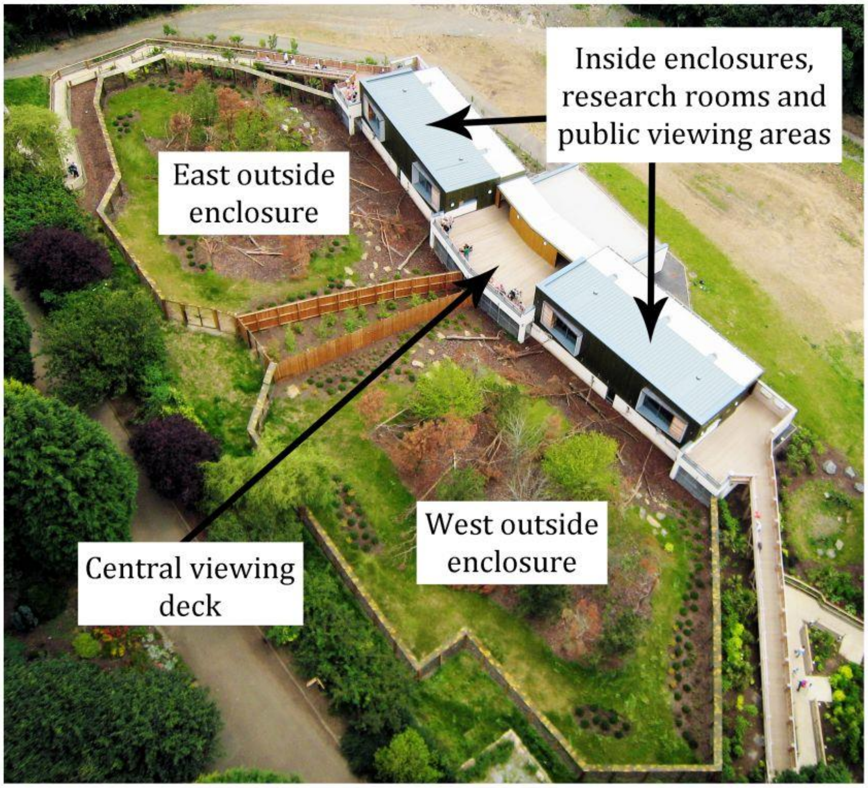


Figure 2. The Living Links facility.

Capuchins are able to access the outdoor enclosure three different ways: 1) through a doorway directly connected to their indoor enclosure, 2) through off-show "holding cages" (239cm x 150cm x 214 cm), which are connected to their indoor/outdoor enclosures via a mesh tunnel, and 3) through the research cubicles (see Figures 3 and 4). The monkeys usually have near-permanent access to all of these areas except on certain occasions (e.g. cleaning the enclosures, or during certain experimental setups); data collected for this study, however, only took place when study subjects had full access to both their indoor and outdoor enclosures.

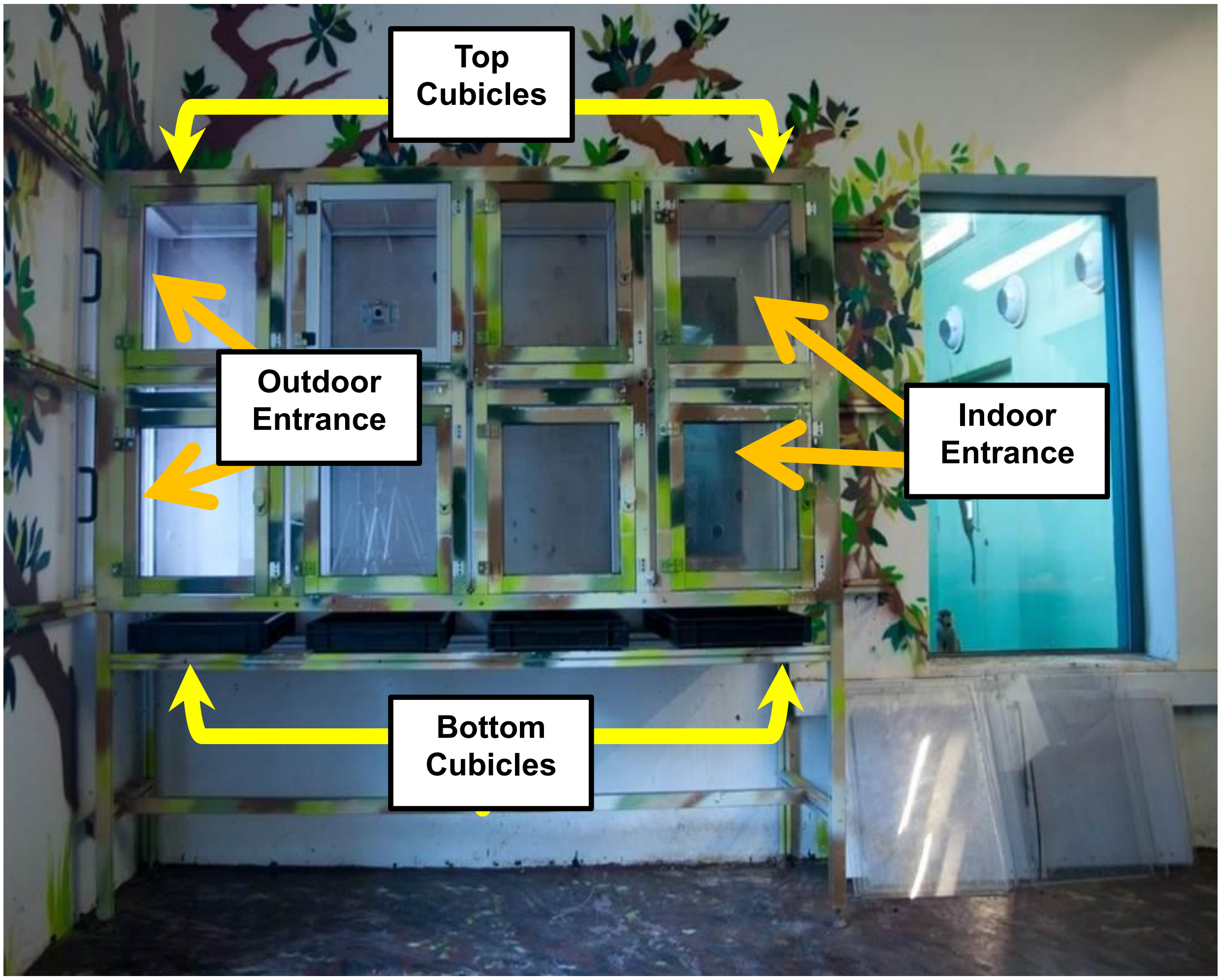


Figure 3. Diagram of the research cubicles for East group. The West group cubicles were designed exactly the same.

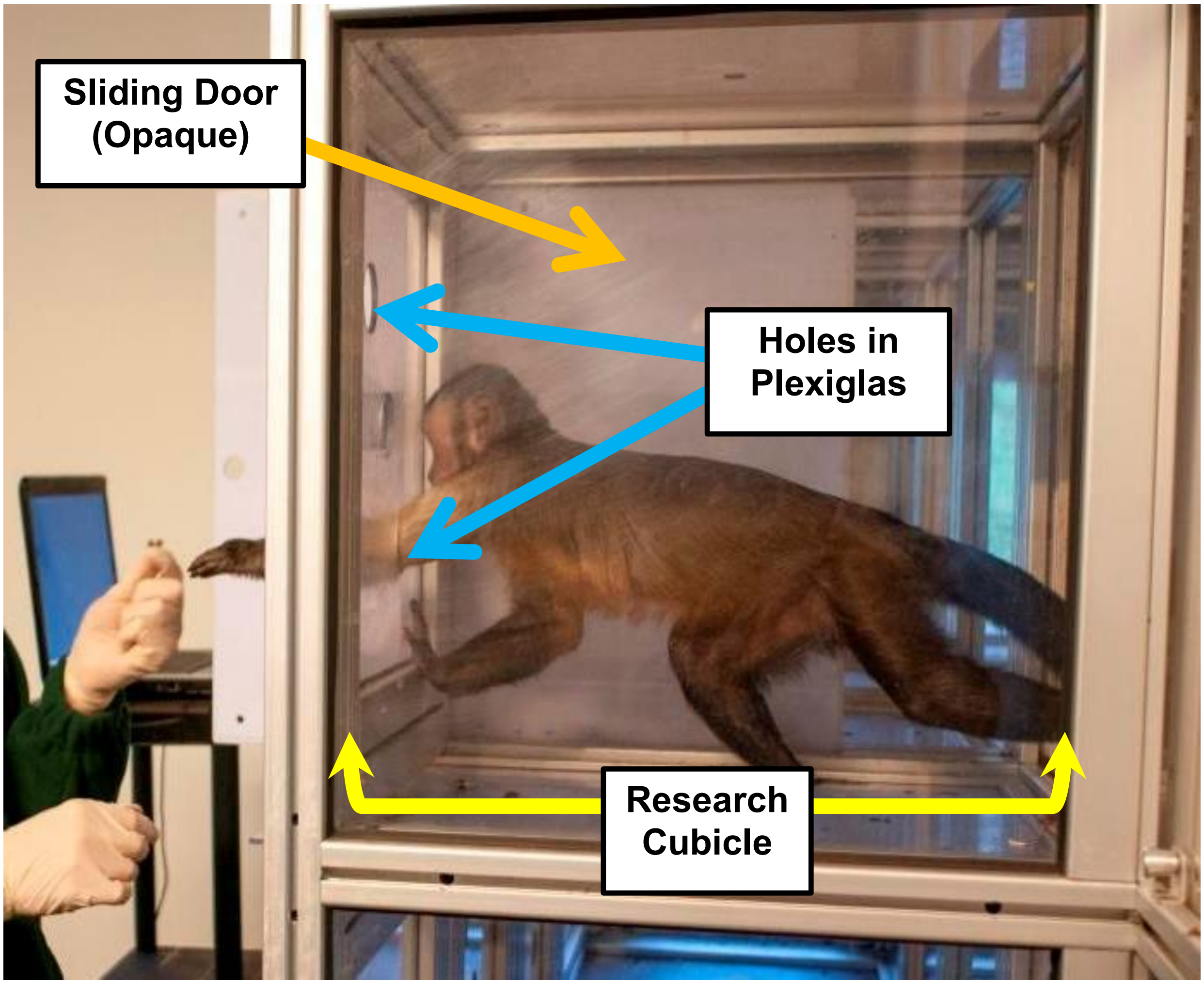


Figure 4. Diagram depicting a monkey inside one of the research cubicles.

The “East” capuchin group contained 4 adult males, 3 adult females, no sub-adults, 1 juvenile, and 3 infants (following age-sex class definitions in Table 1 from Fragaszy et al. 2004). The “West” capuchin group contained 4 adult males, 3 adult females, no sub-adults, 4 juveniles, and 1 infant. One adult male (Maurice) died during this study and was included in the personality analysis (Chapter 3) but not the remaining chapters. The pedigrees for both the East and West groups are provided in Figures 5 and 6. Coefficients of relatedness (r) (hereafter “kinship”) were estimated between each monkey using the monkeys’ pedigrees, whereby r=0.5 for parent-offspring relations, r=0.5 for full sibling relations, r=0.375 for ¾ siblings (e.g. cases of inbreeding), r=0.25 for grandparent-grandchild relations, r=0.25 for aunt/uncle-nephew/nice relations, r=0.125 for half siblings, and r=0.125 for first cousins. Kinship calculations are provided in Tables 1 and 2 of the Appendix.

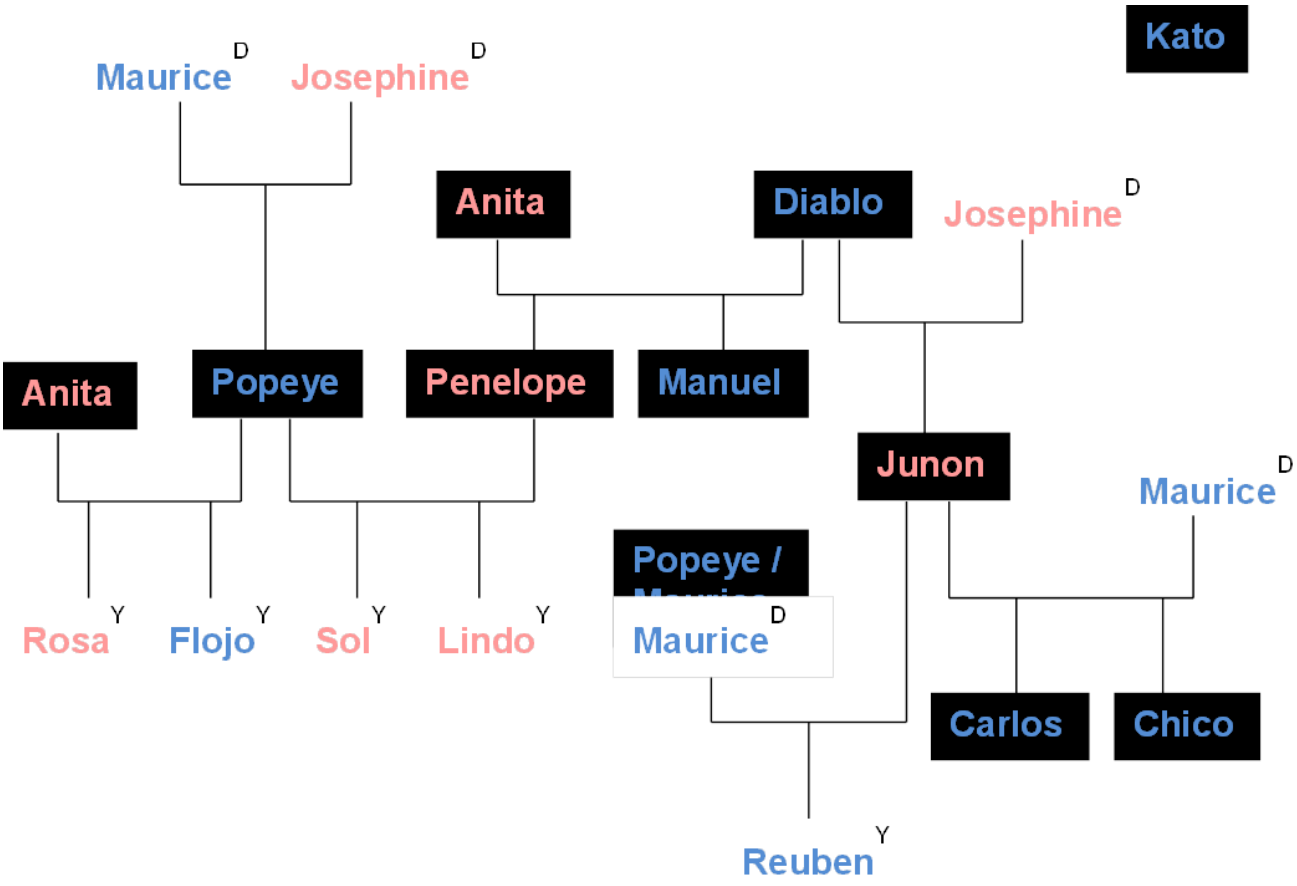


Figure 5. Pedigree for the East group capuchins. Pink names = females, Blue names = males, names labelled in black were the “East Group” subjects of this thesis. Y=young, <1y.o. D=deceased.

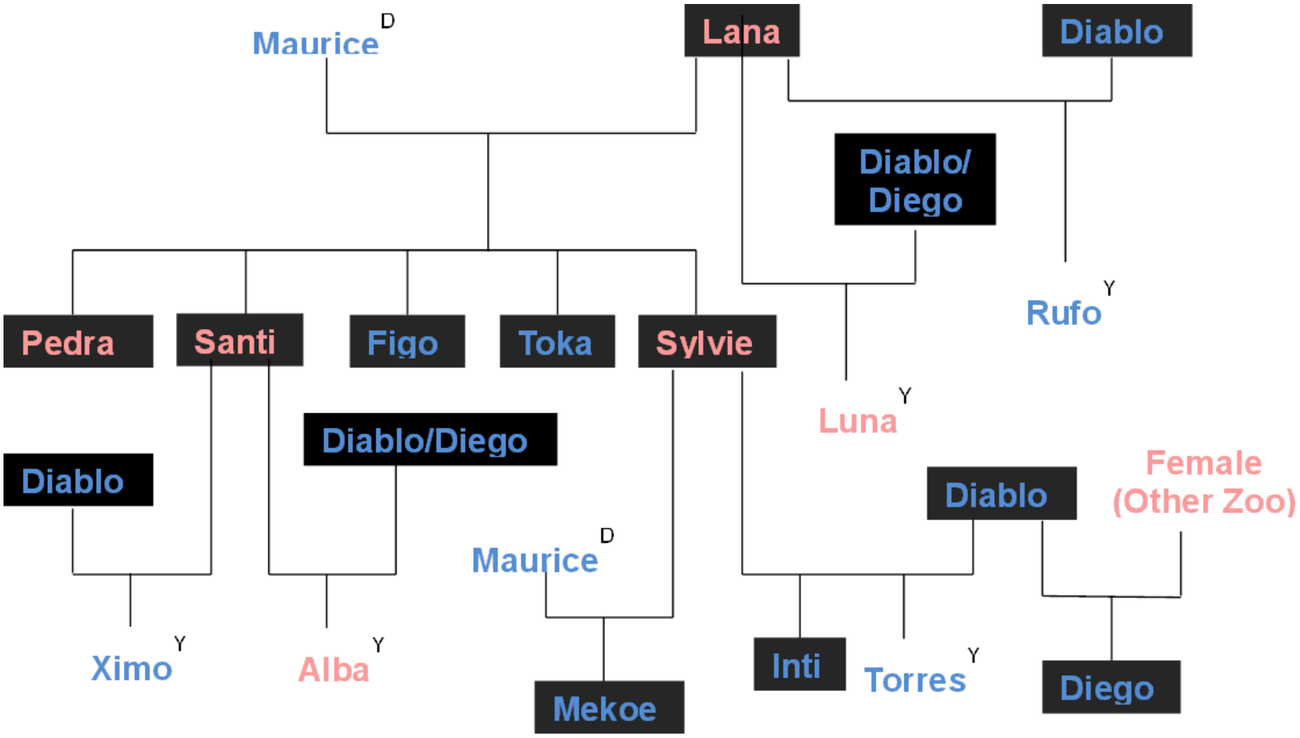


Figure 6. Pedigree for the West group capuchins. Pink names = females, Blue names = males, names labelled in black were the "West Group" subjects of this thesis. Y=young, <1y.o. D=deceased.

Age of the study subjects ranged from 2 to 40 years for males (average 11.17 ± 13.72 years, N = 12 capuchins), and 3 to14 years for females (average 8.86 ± 3.63 years, N = 7 capuchins). Infants dependant on their mothers (i.e. <1yo) were not included in data collection. All group members were captive born and mother-reared except an adult male from East group, who was wild-born and hand-reared by humans, and the original wild-born alpha male of West group; both wild-born individuals came to LL as established members of their group (Dufour et al. 2011). All monkeys received pre-measured commercial TrioMunch pellets supplemented with fresh fruits/vegetables three times daily, and were given cooked chicken and hardboiled eggs weekly. Dried fruits/nuts and live insects were occasionally scattered throughout the monkeys' enclosures at random times throughout the week. Water was available *ad libitum* at all times. Further housing and husbandry details are provided in Leonardi et al. (2010).

2.3.3. Training Monkeys to Engage in Research within Cubicles

Beginning in 2008, the capuchins were trained to walk inside the research cubicles that are connected to their indoor/outdoor enclosure via two doorways (one doorway leading from the indoor and outdoor enclosure, respectively). Using positive reinforcement (i.e. offering food rewards), monkeys were trained to comfortably sit or stand within the cubicles either by themselves or with other members of their group. Over time, monkeys were trained to allow the experimenter to close them inside a single cubicle (49.5cm X 52.1cm x 51.4cm) using either opaque or transparent sliding doors, thereby separating them from the rest of the group. The sliding doors could be completely removed, transforming the cubicles into a long passageway, or could be inserted into grooves between each cubicle, resulting in a total of eight single-unit cubicles in which monkeys could be separated from one another for testing (Figure 3). A maximum of four single-unit cubicles could be formed on the top and bottom row of the cubicles, respectively (Figure 3). Each of these cubicles is large enough to enable the occupant to have sufficient space to move around. One important aspect of the monkeys' training was for them to learn that by either gesturing or touching one of the closed sliding doors, the experimenter would open the door to give that individual the option of walking freely back into their main enclosure (i.e. "free-choice" participation). For welfare purposes, free-choice participation is still strictly enforced at LL for all studies in which monkeys are required to be closed-off within the cubicles. Thus, in the present study, subjects could choose to end a session prematurely before the experimenter was done with testing, and only those subjects who chose to enter cubicles underwent testing.

2.4. Data Collection

2.4.1. Behavioural Sampling

Fifty-four hours of focal observations were recorded over a 4-month sampling period (May to August, 2011), totalling 3 hours for each member of East and West group. Behavioural data collection began four months after completing the first learning task and one month after completing the second learning task (see Section 2.4.4). Thus, behavioural measures were considered representative of subjects' social status and behaviour at the same time when their learning abilities were assessed.

The behavioural activities of each monkey were recorded for 10 minutes per day (see Table 2 for behaviours and definitions). Subjects were sampled evenly across all periods of the day, usually between 9:00 and 17:30. Incidences of aggression, coalitionary support, scrounging, and food sharing initiated/received by each focal monkey were recorded continuously throughout the sampling period, while all other behaviours were recorded at 1-min intervals using point sampling methods (Martin and Bateson 2007). In all cases of social interaction, the actor(s) and recipient(s) were noted. In each point sample, all group members within two body lengths from the focal monkey were recorded. If no monkey was within two body lengths, the focal was described as "solitary". Two body lengths was used as a cut-off point since this appeared to be the minimum distance an individual allowed another individual to approach before they reacted (e.g. stay or move away; pers. obs.). Spatial proximity data from a dyadic matrix were used to calculate the social network position of each subject at the time their learning abilities were assessed. Each monkey's raw data for each behavioural category can be found in Table 3 of the Appendix.

Table 2. Behaviours Recorded During Focal Sampling.*

Behaviour	**Definition**
Aggression	Open-mouth threats, vocal threats, lunging, chasing, hitting, and/or biting.
Alert	Visually scanning surroundings, head and body erect/tense.
Coalitionary support	Another individual intervenes during a conflict between two parties, clearing directing aggression towards only one of the combatants.[1]
Feeding	Searching for, or ingesting food.
Food sharing	One individual allows another individual to take pieces of its food (from hands or mouth).
Grooming	Picking through the hair of another individual.
Moving	Locomoting from one point to another.
Playing	Wrestling, gymnastics, hitting, or chasing without intended aggression.[2]
Resting	Lying down or sitting, not exhibiting any other behaviour.
Scrounging	Exploiting food found by others; successful begging or stealing food from others.[3]
Solitary	No monkey within two body lengths away from the focal.
Vigilant	Monitoring the activities of particular individual(s) (e.g. humans or other monkeys), usually from a high or exposed vantage point.

[1]Ferreira et al. (2006); [2]Burghardt (2005); [3]Arbily et al. (2010)

For statistical analyses, continuously-recorded behaviours were represented in terms of the total number of events observed across sampling periods, while behaviours recorded via point sampling were represented in terms of the proportion of time individuals spent engaged in each behaviour when in view. These data were used to calculate relationship quality scores for each monkey (see methods in Chapters 4 and 5).

2.4.2. Puzzle Feeders

Between 15 May and 8 June, 2011, five puzzle feeders were introduced to the outdoor enclosures of East and West groups. All group members could freely interact with the feeders. Each feeder was made out of a cylindrical piece of white piping (length: 76.2cm, diameter: 5.08cm), with approximately 8-10 holes drilled into it (Figure 7). Each hole was 2.5 cm in diameter. Feeders were attached vertically to trees within the group's outdoor enclosure, and spaced no further than 10 meters from each other. Figure 8 shows the location of each feeder within each group's enclosure. For each feeder, the bottom of the pipe was left open while the top of the pipe was closed (Figure 7). Ten paper packets, each containing five raisins, were placed in the top portion of each feeder, and wooden sticks were inserted into the holes of the pipes to prevent the packets from falling out from the bottom. This prevented subjects from accessing the paper packets in the top portion of the pipe, but allowed the packets to drop freely from the pipe once all the wooden sticks had been removed.

Feeders were introduced four days a week for approximately 30 minutes per day, or until all of the puzzle feeders had been solved. During sessions, all instances were recorded in which a monkey approached another monkey at a feeding site, noting whether the receiving monkey responded to their approach by either avoiding or staying at the feeder within the first 10 seconds of being approached. East group underwent 8 sessions, and West group underwent 10 sessions. These data were used to calculate avoid-stay symmetries in calculations of relationship quality (see Chapters 4 and 5).

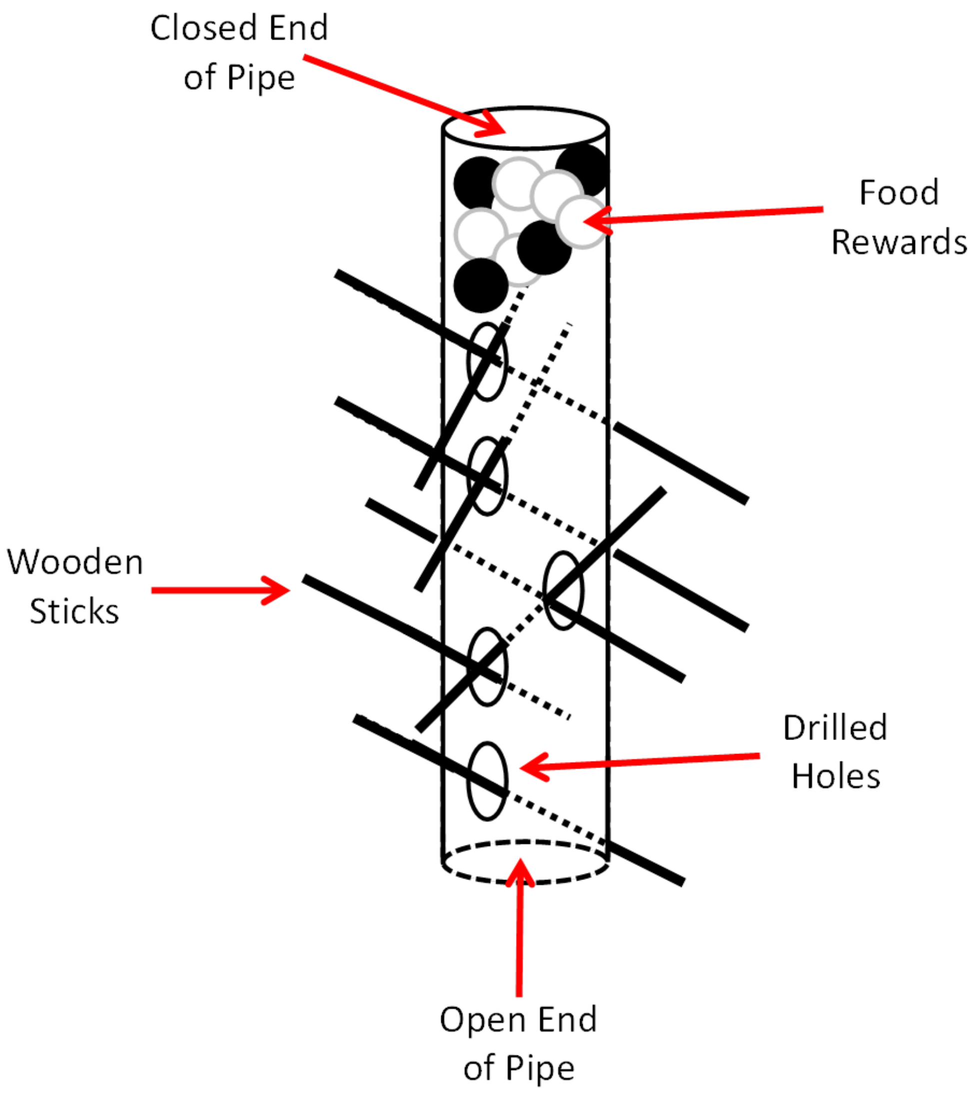


Figure 7. Diagram illustrating the design of each puzzle feeder introduced to the outdoor enclosure of East and West groups.

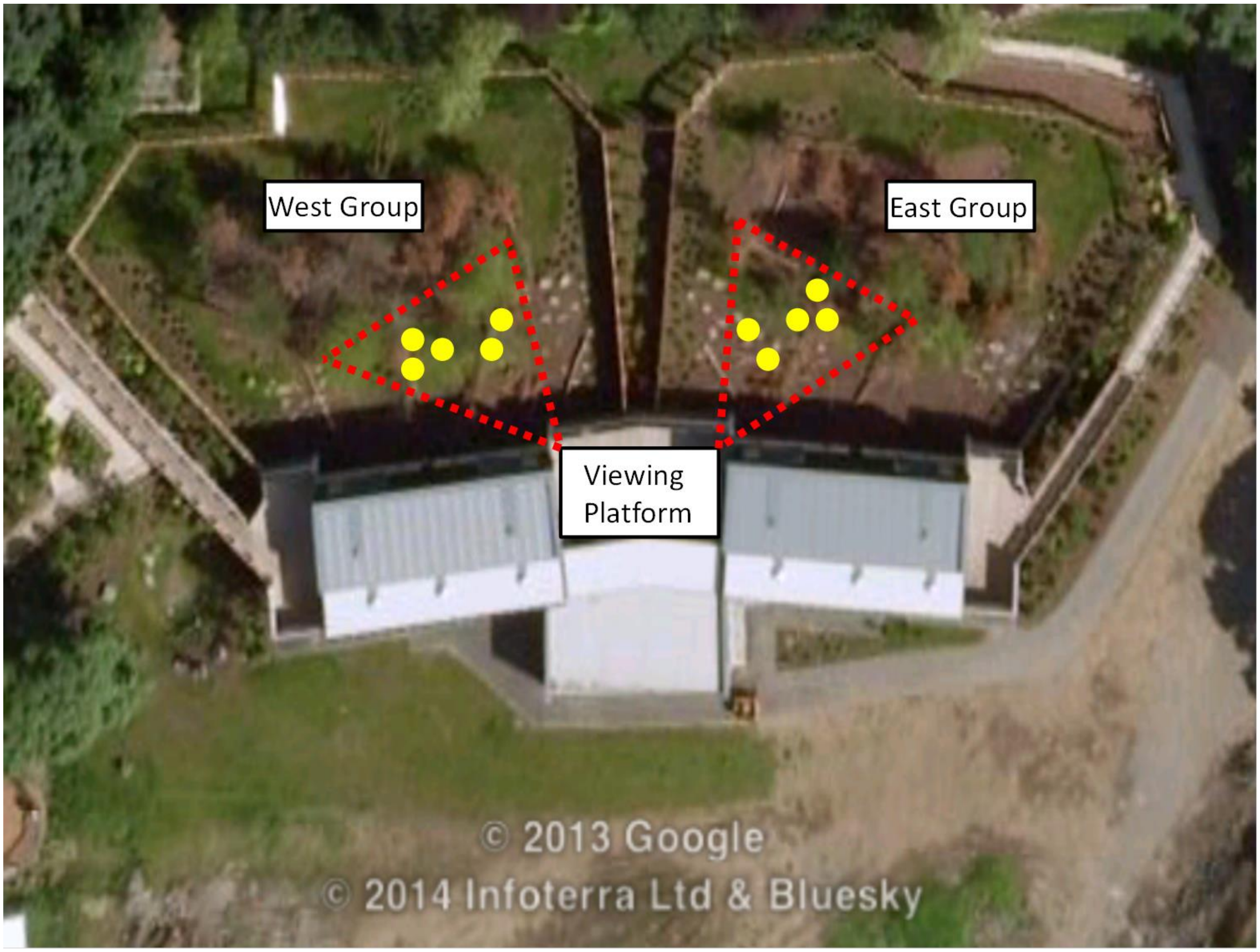


Figure 8. Bird's-eye view of Living Links. Yellow dots indicate where each puzzle feeder was positioned within the East and West group's outdoor enclosure. The dotted triangles indicate the field of view from which the observer recorded monkeys' approaches and displacements from the puzzle feeders.

2.4.3. Personality

To assess personality in capuchins, human raters completed the Hominoid Personality Questionnaire (Weiss et al. 2009) on 127 monkeys spread across seven international sites. Each monkey was rated only by those raters with at least one year of experience working directly with those monkeys. Further details on the study sites, study subjects, and number of human raters per monkey can be found in Chapter 3. The HPQ template is provided in the Appendix; it can also be found online at: http://extras.springer.com/2011/978-1-4614-0175-9/weiss_monkey_personality.pdf. The HPQ has previously been validated in other primate species, such as rhesus macaques (Weiss et al. 2011), Barbary macaques (*Macaca sylvanus*; Konečná et al. 2008, 2012), orang-utans (*Pongo spp.*; Weiss et al. 2006; Weiss et al. 2012), and chimpanzees (Weiss et al. 2009, 2012). Of the 54 items in the questionnaire, 40 were sampled from Goldberg's (1990) Big Five taxonomy while the remaining items were developed by King and Figueredo (1997) and Weiss et al. (2009) specifically for the purpose of rating nonhuman primates. All traits included in the HPQ capture a broad range of behaviours relevant to most species of primate including brown capuchins.

The HPQ instructs raters not to discuss their ratings with others, and to answer each of 54 items on a seven point scale. For example, a score of '1' was defined as "Displays either total absence or negligible amounts of the trait". A score of '7' was defined as "Displays extremely large amounts of the trait".

The layout of the HPQ is similar to those used in other studies of primate personality (Stevenson-Hinde and Zunz 1978; Weiss et al. 2007), particularly the well-known Madingley Questionnaire (Stevenson-Hinde and Zunz 1978; Stevenson-Hinde and Hinde 2011). The HPQ was chosen over these other questionnaires because it covers a more eclectic range of traits. For example, the Madingley questionnaire is considerably lacking in adjectives relevant to conscientiousness-like traits (e.g. distractible and perceptive). Each item in the HPQ consists of an adjective paired with one to three sentences defining it within the context of primate behaviour. For example, *fearful* was defined as "Subject reacts excessively to real or imagined threats by displaying behaviours such as screaming, grimacing, running away or other signs of anxiety or distress”. The LL capuchins were rated for personality between May-August 2010.

Test-retest reliabilities were examined for a sub-sample of the original raters in order to determine how consistent raters were over time. Cronbach’s alpha (Field, 2009) was used to compare ratings made by each rater at two time periods: when they originally filled out the forms and one year later. Raters were not informed in advance that they would be asked to re-rate monkeys.

Two intra-class correlations were calculated to determine inter-rater reliabilities for subjects rated by at least two raters (Shrout and Fleiss 1979). The first, $ICC(3,1)$, indicates the reliability of individual ratings. The second, $ICC(3,k)$, indicates the reliability of the mean of k ratings. Following Weiss et al. (2011), any items with inter-rater reliabilities equal to or less than zero were considered unreliable and excluded from further analyses.

Similar to the item-level test for inter-observer reliabilities, for those subjects that were rated by at least 2 raters, the inter-rater reliability of components was assessed using Shrout and Fleiss’s (1979) $ICC(3,1)$ and $ICC(3,k)$. To determine the internal consistencies, Cronbach’s alpha was calculated for each component in the total sample using the alpha function (Revelle 2011). Cronbach’s alpha values lower than 0.7 were deemed as unreliable (Field 2009).

Following previous work on primate personality (e.g. Weiss et al. 2009, 2011), reliable raters’ scores on each of the 54 items were averaged for each individual monkey, and principal components analysis (PCA) was used to reduce these mean ratings down to their principal domains of personality. The number of components to extract was determined by examining the scree plot and conducting a parallel analysis (Horn 1965) using the paran function (Dinno 2008). Although the ratio of items to subjects was outside the recommended range for PCA, recent simulation studies have found that stable personality structures can nevertheless be derived even when sample sizes are considerably small (de Winter et al. 2009). Likewise, a study of Barbary macaques (Konečná et al. 2012) demonstrated that the personality structure obtained via a PCA of 26 subjects was highly similar to that derived via regularized exploratory factor analysis, a factor extraction method devised specifically for cases in which the sample size is very small (Jung and Takane 2008; Jung and Lee 2011). Components were rotated using both varimax and promax procedures, and following previous studies, loadings ≥ |0.4| were considered to be salient (i.e. items that explained ~20% of variance within the component; Field 2009; Weiss et al. 2006, 2009, 2011).

Components were interpreted based on the items onto which they loaded and their association with recorded behaviours. Behavioural correlations also served to validate components. The methods used to behaviourally validate each personality component are discussed in further detail in Chapter 3.

Z-scores were calculated for each component (Field 2009); monkeys' scores on each component reflected individual differences in their expression of that particular personality trait (Morton et al. 2013).

2.4.3.1. Limitations of Questionnaires and Alternative Methods to Assess Personality

There is some debate as to whether questionnaire-based assessments of individual personality are more or less representative of personality traits than other methods such as experiments (e.g. introducing novel objects to subjects; Gartner and Powell 2012; Carter et al. 2012) or behavioural observations (Uher et al. 2008; Uher and Asendorpf 2008). The questionnaire method relies on the ability of human observers to accurately describe individuals based on their knowledge and experience of that particular monkey. “Subjectivity” of people’s perception of traits is addressed by statistically cross-validating each participant’s ratings, and incorporating only the cross-validated traits into a PCA which reduces traits into their related principal domains. The personality scores extracted from the PCA can then be correlated with relevant behavioural codings using a sub-set of the original study subjects, thereby providing a further test of validity. For example, an individual who scores highly on a personality component reflecting status might be expected to be frequently engaged in dominance behaviours. Similarly, a sociable individual would be expected to be more socially embedded within their group compared to less sociable individuals.

The questionnaire-based method was selected over other alternative methods because it is an efficient way of gathering data on a large number of traits. Despite mixed opinions as to how accurate and replicable results are (reviewed in Uher et al. 2008), it has nevertheless been validated in many published studies as a reliable method to describe personality traits, therefore indicating that this method sufficiently detects ‘real-world’ personality characteristics in individuals (reviewed in Freedman and Gosling 2010). One alternative method would be to record behaviour, and define personality traits according to the frequencies of those behaviours (Uher and Asendorpf 2008). However, this method limits the number of traits one is able to assess within a reasonable course of time, and results can easily be biased by outside disturbances or sampling intensity and duration.

2.4.4. Learning Tasks

The LL monkeys can volunteer to participate in non-invasive cognitive and learning experiments during morning and afternoon sessions four times a week (Monday, Tuesday, Thursday, Friday). On each research day, each group undergoes a morning session from 8:30 to 10:30, and an afternoon session from 11:00 to 13:00. Typically, due to scheduling demands from other researchers, each group undergoes testing on a particular experiment per day (either the morning or afternoon session). Since the establishment of LL in 2008, subjects have been involved in a number of cognitive studies, with a wide array of methodological designs (see MacDonald and Whiten 2011); however, the tasks and methods of administration in the present study had not been used before.

All monkeys (N=18, excluding infants) were given the opportunity to engage in two simple discrimination learning tasks. Tasks were conducted over a six-month period, from November 2011 to April 2012. Testing took place in research cubicles, which were divided into two compartments (both 54.6cm x 66cm x 71.1 cm) and separated by a transparent plastic door that was halfway open. Participating monkeys could freely walk between the two compartments. For each task, monkeys were required to learn a simple rule.

Task 1 was conducted between 8 November 2011 and 13 January 2012. During each trial, a food reward was randomly placed in front of one of two compartments (Figure 9a). Compartments were separated by a transparent door that was half-way open, and monkeys could walk freely between them. The location of the food reward (left or right compartment) was randomly selected for each new trial. The goal was for the monkey to learn that by walking and sitting in the compartment that had the food directly in front of it, the researcher would hand them the food. If the monkey failed to do this, no food was rewarded, and the trial was ended. Monkeys received a maximum of 12 trials per session, with each trial separated by 5-7 seconds.

Task 2 was conducted between 15 February 2012 and 1 April 2012. During each trial, two white-opaque cups were placed in front of the monkey (Figure 9b). Each cup was placed directly in front of one of two compartments. Compartments were separated by a transparent door that was half-way open, and monkeys could walk freely between them. The position of each cup (left or right compartment) was randomly selected for each new trial. The two cups differed in size, with one cup twice as tall as the other cup. For this task, the goal was for the monkey to learn that by moving and sitting in the compartment facing the larger cup, they would receive a food reward that was located inside the cup. The larger cup was always the ‘winner’, the smaller cup was always the ‘loser’. If the monkey failed a trial, no food was rewarded, and the trial was ended. Monkeys received a maximum of 12 trials per session, with each trial separated by 5-7 seconds.

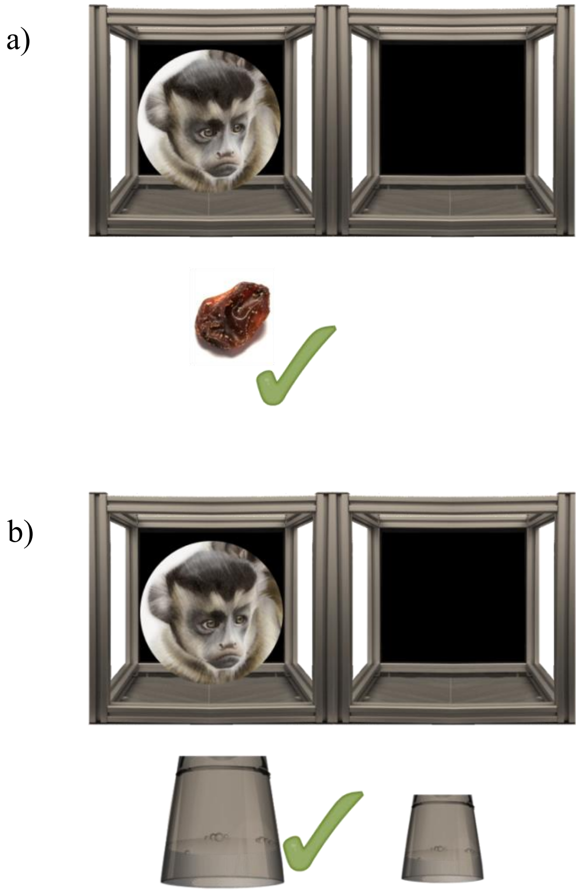


Figure 9. Illustration of a) Task 1 and b) Task 2, which were administered individually to test subjects within research cubicles.

For both tasks, a monkey received 12 trials per session per day until they met learning criteria, or for a maximum of 144 trials (Task 1) and 264 trials (Task 2). For each correct trial, subjects received a food reward (e.g. raisin or piece of papaya). During testing, movements made by the experimenter (F.B.M.) were limited only to setting up each new trial. Temperature and lighting are controlled within the indoor testing enclosures (V. Dufour, pers. com.). Eye gaze of the experimenter during testing was directed at the floor; eye gaze and position of the experimenter behind the apparatus remained the same for each trial to prevent subjects from making “associative cues”. All sessions were video recorded using a SONY 60X HD camcorder mounted 1.5m away from the test subject (and directly behind the experimenter) on a tripod; videos were later coded by the experimenter. Typical of free-choice methods, subjects could control when they wished to initiate or end a session, usually by either gesturing or pressing their hand on the cubicle door exit. If a subject signalled that it wanted to leave, the experimenter stopped the test, opened the door, and released the monkey back into the main enclosure. A binomial test established that subjects would need to score at least 80% of trials (i.e. $\geq$10/12 trials) correctly on a given session for it to be statistically above chance (Morton et al. 2013). Individuals scoring $\geq$80% of trials correctly on three consecutive sessions were considered to have learned the task, and their training subsequently ended.

Participation was calculated for each monkey by dividing the number of sessions they engaged in by the total number of session offered to them, multiplied by 100. The performance of each individual was calculated for each task by dividing the total number of trials answered correctly by the total number of trials undergone, multiplied by 100.

To motivate individual monkeys to participate, highly preferred foods are used while testing (e.g. dried raisins or papaya; V. Dufour, pers. com.). While task performance may potentially be inhibited due to stress-related factors (e.g. Dunko et al. 2007), noises from within the monkeys' main enclosures (e.g. aggressive outbursts; pers. obs.), sex hormone concentrations (Kimura 1996), or other variables, controlling for this variation was beyond the scope of the present study. However, these external biases were minimized by testing participants on two different tasks to derive an average overall score (i.e. "average task performance"; Chapter 7 and 8). Previous work has shown that noise from within subjects' social groups while they undergo testing has little impact on their performance (Worsham and D'Amato 1973). As noted previously, all of the capuchins have been trained since 2008 to undergo testing within the research cubicles, and given that subjects volunteer themselves for testing, this further reduces the possibility that subjects' performances are influenced by stress or a lack of motivation at the time of testing. Finally, female capuchin monkeys give clear behavioural cues when they are cycling (e.g. emitting regular "oestrus" calls and soliciting the alpha male; Fragaszy et al. 2004), and these subjects never participated in testing until they had completed their cycle.

2.4.4.1. General Learning Ability

Although the present study measured subjects' learning ability using two operant tasks within the physical domain, multiple studies have shown that individual differences in animals' performances on operant tasks from both the physical and social are correlated; meaning, individuals that perform well on one particular task are likely to perform well on other tasks as well. Indeed, although general learning ability was not the aim of the present study, those individuals that performed highly on Task 1 were also those that performed highly Task 2 (see results of Chapter 7). The concept of general-domain learning is discussed further in Chapter 7.

Traditional approaches to measuring learning within the social domain, such as matching-to-sample tasks using visual media depicting social situations (e.g. photos of conspecifics engaged in various affiliative/agonistic acts; Bovet and Vauclair 2000), tasks measuring subjects' capacity to learn through demonstration (Carter et al. 2014), or studies on vocal discrimination (Pfefferle et al. 2013), were difficult to use in this study. Recent work has shown that capuchins do not perceive visual media as real, thereby making it difficult to infer what their responses to such stimuli mean within an ecologically valid context (Morton et al. under review). Learning through demonstration can also be affected by subjects' relationship quality with the demonstrator (Pongracz et al. 2008), and although it would have been possible to train demonstrators on a task then pair them with subjects who were similar in rank, this would have considerably reduced the sample size (and thus statistical power) of this study. Additionally, if each pair of monkey was trained to solve a different task, this would have made the amount of time needed to measure subjects' learning performance four-fold (i.e. training on two tasks, learning two tasks), which was beyond the time limits of this study. Lastly, capuchins do not always spontaneously attend to auditory cues when performing tasks (Paukner et al. 2009), and the use of auditory playback methods would have required an extensive study to test the ecological validity of this method for capuchins (which may not perceive recorded sounds in the same way as humans; D'Amato 1988).

In light of evidence supporting the existence of a general learning ability in animals including primates, the tasks used in this study were selected because they made it possible to measure individual differences in learning performance within a reasonable time frame, and were well within the learning capacity of capuchins (see Section 2.2.4).

2.4.5. Social Networks

Social network analysis (SNA) was used to generate association indices between group members. SNA has been increasingly used in studies of animal behaviour, such as studies of disease/social information transmission and social structure (Whitehead, 2008; Hoppitt and Laland, 2011; Lehmann and Ross, 2011; Rushmore et al. 2013). Because individuals that share a relationship with each other can influence the relationships of other individuals within the same network, SNA provides a dimensional approach to measuring the social interactions that occur between individuals within a population (i.e. social "connectivity" between individuals; Whitehead 2008; Croft et al. 2008).

Data for the social networks of both East and West groups were analysed in SOCPROG 2.4 (Whitehead 2009). Although alternative network packages exist (e.g. UCINET), SOCPROG was selected given that it is one of the most popular network package used among animal behaviourists, which facilitates cross-study comparisons, and is also the most user-friendly (Whitehead 2008, 2009). Eigenvector centrality (or "centrality") was calculated for each monkey within their group's network. Centrality not only measures how well each individual is linked in its associations with other individuals, but also how well its close associates are themselves linked (Croft et al. 2008). Centrality is therefore an ideal measure of capuchins' social success as defined in this study (i.e. "social embeddedness").

Spatial proximity is a reliable indicator of relationship quality in animals, including capuchins; individuals that spend much of their time in close proximity typically engage more often in affiliative acts (e.g. grooming and coalitions) than agonistic acts (Janson 1990; Fragaszy et al. 2004; Ferreira et al. 2006; Daniel et al. 2009; Tiddi et al. 2011). Therefore, spatial proximity data (see Chapter 8) were used in the present study as an index of social success, whereby subjects with higher spatial network centrality (i.e. “spatial embeddeness”) were considered more socially successful. Importantly, spatial networks were used as a measure of social success rather than networks constructed from affiliative and agonistic behaviours because there were fewer observations on affiliative/agonistic behaviours (see Table 4 in Appendix) compared to observations of spatial proximity (total 3,240 scans; see Chapter 4). This issue is discussed further in Chapter 6.

Associations were defined using a simple ratio index (Whitehead 2009). This index was chosen over alternative indices (e.g. half-weight or square root which is used when animals are not always visible; Whitehead 2008) given the captive context of this study, i.e. clearly-visible groups. A simple ratio index computes a figure between zero and one based on the number of times two individuals are seen together versus apart, and thus provides a direct measure of how closely associated the dyad is (Whitehead 2008). After setting all of these specifications, the SOCPROG server calculates the network metrics and constructs a sociogram which illustrates the strength of associations between group members.

Given the small sample of monkeys, the robustness of each group’s network was tested by randomly removing 50% of observations, and each monkeys’ centrality was then re-calculated; these new centrality scores were then correlated with those calculated using 100% of the data. For both networks, removing 50% of the data and re-running the analysis yielded scores that were highly correlated with scores calculated using 100% of the data ($r=0.987$, $P<0.001$, $N=18$). Thus, the networks calculated for both groups were considered robust.

2.4.6. Social Rank

Social rank (defined here in terms of one's competitive ability; Bernstein 1981) was determined by calculating David's Scores (DS) using data on the win/loss outcomes of each monkey's agonistic interactions (see "Behavioural Sampling"). Individuals that retreated from other player(s) were considered the "losers" during aggressive encounters (Bernstein 1981). The DS method was used because it takes into account the relative strength of each player (Gammell et al. 2003). Following Hemelrijk et al. (2005), monkeys were organized into a matrix whereby the "winners" of aggressive interactions were labelled on the Y-axis and the "losers" were labelled on the X-axis. The proportion of wins/loses were calculated for each dyad by dividing the number of wins/loses by the total number of interactions observed within each given dyad. Each cell within a given row represented the proportion of "wins" observed for each monkey within a given dyad, while each cell within a given column represented the proportion of "loses" observed for each monkey within a given dyad. Next, the proportions were summed across each row and column to yield an overall ratio of wins/loses for each monkey within the matrix ("*w*" and "*l*", respectively). For each monkey (*i*) along the Y-axis of the matrix, each of the *w*'s of the other monkeys were multiplied by *i*'s winning proportion within that respective dyad, and summed these scores to yield an overall weighted score for *i* (labelled "*w2*"). For each monkey (*j*) along the X-axis of the matrix, each of the *l*'s of the other monkeys were multiplied by *j*'s losing proportion within that respective dyad, and summed these scores to yield an overall weighted score for *j* (labelled "*l2*"). To calculate the DS for each monkey within the matrix, the following formula was used: DS = $w + w2 - l - l2$ (David, 1988). Each monkey's DS score and the raw matrix calculations for the East and West groups are provided in Tables 5-8 in the Appendix.

The number of aggressive events recorded during this study was relatively small (Tables 5 and 7 in Appendix), which reflects the generally low frequency of agonisim among capuchin groups (Cooper et al. 2001; Fragaszy et al. 2004). The robustness of monkeys' rank was therefore tested by removing 50% of observations and recalculating each subject's DS. These scores were significantly correlated with scores calculated using 100% of the data ($r=0.997$, $P<0.001$, $N=18$), indicating that rank calculations were robust.

2.5. Statistical Analyses

Parametric tests were used for all normally distributed data. Each set of data was tested for a normal distribution by dividing the skewness of the data by the standard error of the skewness; if the quotient was <3.0, it was considered to be normally distributed (Weiner et al. 2012). In cases where data were not normally distributed, they were normalized using a log transformation (Field 2009); the use of this method is indicated where appropriate in each chapter.

Principal components analysis (PCA) was used for analyses of personality and social relationship structure (Chapters 3 and 4). This method was chosen because it reduces potentially correlated variables down to their principal domains, thereby resulting in fewer variables (Field 2009). The statistics literature includes a range of recommendations regarding the minimum sample size necessary to run a PCA, such $N\geq300$ (Comrey and Lee 1992) or having a fixed ratio between the sample size and number of variables (e.g. minimum ratio of 5; Gorsuch 1983). A fundamental misconception, however, is that such recommendations are invariant across studies, whereas common rules of thumb regarding sample size are usually not valid or useful (MacCallum et al. 1999). In a review by MacCallum et al. (1999), it was demonstrated through

Monte Carlo simulations that a PCA in which the final solution contains a relatively small number of components with moderate to high communalities (synonymous with R^2), investigators can be confident of the robustness of their results.

As noted in Section 2.4.3, two intra-class correlations (ICC[3,1] and ICC[3,k]) were used to test rater reliability as well as inter-rater reliability of components on personality ratings (Shrout and Fleiss 1979). To determine the internal consistencies of personality components, Cronbach's alpha was calculated for each component in the total sample using the alpha function (Revelle, 2011); cronbach's alpha values lower than 0.7 were deemed as unreliable (Field 2009). In Chapter 3, an Everett test (Everett 1983) was used to help determine how many components to retain, and targeted orthogonal Procrustes rotations were used to compare different component solutions (McCrae et al. 1996).

Pearson correlations were used to test for significant relationships between two variables (Field 2009); partial correlations were used to control for specific variables when testing for correlations between variables (Field 2009). Residual scores from regression analyses between dependent and independent variables were also used to control for possible effects of dependent variables on the independent variables (Field 2009). T-tests were used to test for significant differences in the means of two variables. Where the sample size differed between variables, boot-strapped t-tests were used (replacement=1,000 permutations; Ahad et al. 2012). Dependent variables were entered into a multiple regression model to test for their relative contribution to variation in independent variables (Field 2009). Data for grooming, a behavioural state, were subjected to a log survivorship analysis to determine how many statistically separate bouts of grooming existed within the dataset (following Martin and Bateson 2007; see Figure 1 in Appendix for log survivorship curve). Bootstrapped Pearson correlations were used for analyses where pseudo-replication was an issue (see Chapter 5). The use of each statistical method is indicated where appropriate within each chapter. Significance tests were two-tailed with critical values of 0.05; considering the small sample of monkeys in this study, effect sizes were also taken into account when interpreting results (Field 2009).

2.7. Ethical Statement

This study was non-invasive and complied with guidelines of the Association for the Study of Animal Behavior (ASAB 2012). This research was also approved by local ethics committees, including the Living Links Research Review Committee and the Research Ethics Committee within the Psychology department of the University of Stirling. No animals were physically harmed, and all precautions were taken to prevent psychological disturbance and exposure to potential human illness (e.g. wearing latex gloves and a face mask) when working with the monkeys in the research cubicles.

CHAPTER 3

Personality Structure in Brown Capuchin Monkeys

Photograph 3

CHAPTER 3

Personality Structure in Brown Capuchin Monkeys

This chapter is based on work published as Morton et al. (2013), and is the result of a collaboration between ten researchers from seven research sites (see Appendix for publication). Here I outline the utility of this approach for testing the hypotheses examined in this thesis.

3.1. Introduction

Animal personality is often defined as individual differences in behavioural consistency across time and context (Gosling 2001; Carere and Eens 2005). For instance, individual measures of boldness in bluegill sunfish (*Lepomis macrochirus*) are stable across multiple environments, and are replicable in the same subjects after a 1 to 3 month re-capture period (Wilson and Godin 2009). Similarly, Capitanio (1999) found that in rhesus macaques (*Macaca mulatta*), individual scores on sociability were associated with differences in affiliative behaviour up to several years later, and in situations that were different from those in which monkeys' personalities were originally assessed.

Although the existence of personality in animals has been critiqued and labelled as "noise" deviating from behavioural norms (discussed in Tooby and Cosmides 1990), studies have shown that such traits can be heritable (van Oers et al., 2005; Adams et al. 2012) and predict life history patterns (e.g., metabolic rate, reproduction, health, and longevity; Cavigelli et al. 2008; Careau et al. 2009; Capitanio 2011; Weiss et al. 2012). For example, in humans, heritability estimates of personality traits generally range from 0.4 to 0.8 (Riemann et al. 1997; Bouchard and Loehlin 2001), and individual differences in these traits have been linked to the number and quality of offspring reared within families (Alvergne et al. 2010). Additionally, in a population of bighorn sheep (*Ovis canadensis*), Réale et al. (2009) found that individual scores on boldness and docility had heritability estimates of 0.65 and 0.39, respectively; however, unlike more docile sheep, bolder individuals survived longer and had higher reprouctive success later in life. Thus, the idea that animals display consistent and potentially heritable patterns of individual behaviour raises intriguing questions regarding the adaptive function of such traits (Sih et al. 2003; Dingemanse and Réale 2005;).

To date, personality has been studied in many animals, including mammals, birds, fish, reptiles, amphibians, and invertebrates (Gosling 2001). Common approaches to measuring personality in animals include: 1) behavioural codings, whereby behaviours are systematically recorded on focal individuals using an ethogram (e.g. Uher and Asendorpf 2008), 2) subjective personality ratings, whereby multiple adjectives (or “traits”) are rated by observers familiar with the individual animals (e.g. Weiss et al. 2009; Lee and Moss 2011;), and 3) controlled experiments, e.g. recording individual responses to a novel object (e.g. Uher and Asendorpf 2008). In each case, data reduction methods can be used to condense ratings or behavioural codings into one or more dimensions of personality (collectively called personality “structure”; e.g. Weiss et al. 2009). An individual’s score on a given dimension corresponds to their position along a particular behavioural continuum (e.g., the shy-bold axis; Wilson et al.1994).

Observer ratings are most often used to study personality structure, particularly that of behaviourally-complex species such as nonhuman primates (Gosling 2001). Although such methods are subjective, observers often independently agree on their ratings of subjects (Gosling, 2001; reviewed in Freeman and Gosling 2010). The degree of concordance (or agreement) has been statistically validated in numerous studies (e.g. Freeman and Gosling 2010). Additionally, observer ratings usually reflect experimentally and /or ethologically measured behaviours recorded in the same individuals (e.g. Capitanio 1999; Lee and Moss 2011; Manson and Perry 2013). Therefore, rather than being mere reflections of anthropomorphic projection, observer ratings can provide meaningful information about the personalities of animals (Gosling 2001).

Compared to other methods, there are several advantages to measuring personality using observer ratings. For one, unlike experiments and behavioural codings, ratings describe personality in absolute terms and are often generalized across multiple contexts (Carter et al. 2011). Thus, ratings are less likely to be biased by context-specific disturbances, such as subjects' motivation, learning, or sampling intensity/duration (Frost et al. 2007; Biro 2012; Gartner et al. 2012). Additionally, data on a variety of traits can be obtained more rapidly and for more individuals through observer ratings than with other methods, which are then supplemented with experimental data or behavioural codings to test construct validities (Freeman and Gosling 2010). Nevertheless, as with any methodological approach, there are also limitations to using observer ratings. For instance, ratings can be biased towards memory of behaviourally-rich episodes, rather than typical day-to-day activities (Craik 1993). Gosling (2001) points out that different species likely vary in the ease with which observers can reliably rate individuals on multiple traits, particularly if individuals or species are relatively limited in their behavioural repertoire. Observers' perception of certain traits (and thus the extent of inter-observer agreement) may be indirectly influenced by daily communication among raters (e.g. "animal gossip" while at work; but see Funder et al. 1995). Therefore, to demonstrate that observer ratings are reliable and valid, studies must ensure that 1) personality traits rated by observers *independently* agree with one another, 2) observers are consistent in how they rate individual animals (i.e. test-retest reliability), and 3) observers' ratings *independently* correlate with real-world behaviours in the subjects that were originally rated (Kenrick and Funder 1988; Gosling and Vazire 2002; Freeman and Gosling 2010).

This chapter examines the personality structure of brown capuchin monkeys. Capuchin monkeys are one of the most widely distributed genera of New World primate in Central and South America, and are renowned for their social complexity and highly adaptive behaviour in the wild and in captivity (Fragaszy et al. 2004). Studies of the psychology of these animals have mostly focused on their cognitive abilities (e.g. Fragaszy et al. 2004). Platyrrhines (New World monkeys) are only distantly related to catarrhine species, sharing a common ancestor approximately 43 million years ago (Steiper and Young 2006). However, some New World species, including brown capuchins, exhibit behavioural and cognitive similarities (independently derived analogies) to catarrhine species (e.g. tool use, delayed gratification, and social hierarchies; Fragaszy et al. 2004; Deaner et al. 2006; Amici et al. 2008; Addessi et al. 2011). Considering that individual differences in behaviour and cognition are closely associated with differences in personality (Carere and Locurto 2011), comparative studies of personality in Old and New World species may therefore help identify variables within the natural and social world of primates that contribute to the evolution of personality traits and personality variation. To date, however, research on primate personality structure has predominantly been limited to catarrhines, i.e. apes and Old World monkeys (Freeman and Gosling 2010; but see Manson and Perry 2012). Thus, further data are needed on other primate clades.

The first aim of this chapter is to derive personality structure from reliable ratings obtained from a large multi-site sample of brown capuchin monkeys (based on Morton et al. 2013; see Appendix). Ratings of brown capuchins on individual personality traits have been associated with cortisol reactivity (Byrne and Suomi 2002). Human observer ratings appear to capture biologically-meaningful information about this taxon. Until recently, it was unknown whether and how individual traits cluster into personality dimensions in brown capuchins (Morton et al. 2013).

Using a subset of the original study population, the second aim of this chapter is to validate the personality structure derived in brown capuchins by correlating individual scores on each component with behaviours that were systematically recorded up to a year later. As previously discussed, personality in animals is generally defined in terms of consistent inter-individual differences in behaviour (Gosling 2001). Thus, if observer ratings capture behaviourally-meaningful information about subjects within this study, then individual scores on each personality dimension should correlate with relevant behaviours sampled across time and context.

3.2. Methods and Materials

3.2.1. Study Sites and Subjects

Subjects were 127 captive brown capuchin monkeys that were at least 1 year old, belonging to 15 social groups from 5 sites in the United States, 1 site in the UK, and 1 site in France (see Table 3). Across all sites there were 60 males and 67 females. Age ranged from 1 to 40 years and the mean age was 11.0 years (*SD* = 8.9). This study was non-invasive, approved by local ethics committees, and complied with the 2012 regulations of the Association for the Study of Animal Behaviour. Housing conditions of subject from each site are as follows:

Table 3. Age, Sex, and Number of Study Subjects at Each Research Site.

Location	**N**	**Groups**	**Age (mean years ± SD)**	**Sex Ratio (M:F)**
Bucknell University	13	1	8.77 ± 6.18	4:9
CNRS	18	1	13.67 ± 7.84	6:12
GSU	12	2	9.67 ± 5.65	7:5
Living Links, UK	19	2	10.32 ± 10.99	12:7
Living Links, USA	29	2	14.90 ± 11.06	11:18
National Institutes of Health	26	6	8.39 ± 7.33	16:10
Yale University	10	1	7.9 ± 5.28	4:6

Living Links, UK. Nineteen capuchins were from the ‘Living Links to Human Evolution’ Research Centre at the Royal Zoological Society of Scotland, Edinburgh Zoo, UK (MacDonald and Whiten, 2011). These individuals were from two breeding groups, and each cohabited with a group of common squirrel monkeys. Groups were housed in identically designed, mutually exclusive, 189 m^3 indoor enclosures with natural light and near-permanent access to a 900 m^2 outdoor enclosure containing trees and other vegetation, providing ample opportunity to engage in natural behaviours. At the time of this study, the “East” group contained 4 adult males, 3 adult females, no sub-adults, 1 juvenile, and 3 infants (following age-sex class definitions in Fragaszy et al. 2004). The “West” group contained 4 adult males, 3 adult females, no sub-adults, 4 juveniles, and 1 infant. All group members were captive born except an adult male from East group, who was hand-reared, and the original wild-caught alpha male of West group; both of these individuals came to LL as established members of their groups. All monkeys received commercial TrioMunch pellets supplemented with fresh fruits/vegetables three times daily, and were given cooked chicken and hardboiled eggs weekly. Water was available *ad libitum* at all times.

Institute Pluridisciplinaire Hubert Curien, CNRS. Eighteen capuchins belonged to a single group (‘Arnaud’ group) at the Primatology Centre of the University of Strasbourg, France, and consisted of 6 adult males, 12 adult females, 0 juveniles, and 0 infants. All monkeys were captive born except for the eldest female, which was hand-reared and most likely wild-born. The hand-reared female has been a member of Arnaud group since 1987. Monkeys were provided commercial monkey diet pellets and water *ad libitum*, and received fruit once a week. Monkeys were never food-deprived. All subjects were housed in an indoor ($99m^3$) and outdoor ($45m^2$) enclosure, consisting of multiple compartments. Further details in Morton et al. (2013).

Language Research Center, Georgia State University. Twelve capuchins belonged to two groups at the Georgia State University (GSU) in Atlanta, Georgia, USA. The ‘Griffin’ group consisted of 2 adult males, 2 adult females, 2 juveniles, and 0 infants. The ‘Gabe’ group consisted of 1 adult male, 2 sub-adult males, 2 adult females, 1 juvenile, and 0 infants. All monkeys were captive born. For both groups, enclosures consisted of an indoor room (Gabe group: $75.84m^3$; Griffin group: $54.42m^3$) connected to a large outdoor enclosure (Gabe group: $13.51m^2$; Griffin group: $21.15m^2$). Group members spent most of their time in the outdoor area throughout the year, except when engaged in research, during bad weather, or overnight. Monkeys were provided commercial monkey chow three times a day (morning, noon, evening), and fruits and vegetables were given every evening. Water was available *ad libitum* at all times, including during cognitive and behavioural testing. The enclosures were made of chain link fencing and were equipped with swings, ropes, and other materials to create three-dimensional living conditions to enrich the monkeys. The older study subjects had previously been housed together in various combinations at Yerkes National Primate Research Center, before being relocated to GSU 5 years ago. Further details in Morton et al. (2013).

Bucknell Primate Lab, Bucknell University. Fourteen of the capuchins belonged to a single group at Bucknell University in Lewisburg, Pennsylvania, USA. They were housed in one social group consisting of 2 adult males, 2 adult females, 5 sub-adult females, 5 juveniles, and 0 infants. All monkeys were captive born. The enclosure consisted of a series of seven compartments (totalling $630m^3$) made of caging wire, which were interconnected by doorways or tunnels also made of caging wire. The compartments included various perches, swings, and poles to ensure a most naturalistic environment for climbing and movement. Monkeys were provided commercial monkey chow twice per day (morning, evening), fruits and vegetables were given once per day (morning), and an afternoon snack consisting largely of peanuts, raisins, and low-sugar cereal was given in the afternoon. Water was available *ad libitum* at all times. The older subjects (N = 4) had previously been housed at Yerkes National Primate Research Center before being relocated to Bucknell University 12 years ago. Further details in Morton et al. (2013).

Living Links, Yerkes National Primate Research Center, USA. Twenty-six brown capuchin monkeys housed in two separate social groups at Living Links, part of the Yerkes National Primate Research Center. One group consisted of 15 monkeys housed in 25 m^2, and the other of 11 monkeys in 31 m^2. Both groups had access to indoor and outdoor areas and were visually, but not acoustically isolated from each other. The monkeys received Purina monkey chow and water *ad libitum*, and trays containing fresh produce every evening. Monkeys were never food or water deprived and all procedures were approved by the Institutional Animal Care and Use Committee (IACUC) prior to the commencement of the study. Further details in Morton et al. (2013).

Laboratory of Comparative Ethology, National Institutes of Health. Twenty-six capuchins came from two captive breeding group and several small bachelor groups at the

Laboratory of Comparative Ethology, NICHD. At the time of the study, one group (Garth's group) comprised 5 adults (4 female and 1 male, aged 7-30 years) and 4 juveniles (2 female and 2 male, aged 1-3 years). Three infants (1 female and 2 male, aged <6 months) were part of the group but were not rated for the current study. The second breeding group (Manuel's group) comprised 4 adults (3 female and 1 male, aged 5-12 years) and 4 juveniles (1 female and 3 male, aged 2-4 years). A further nine animals were pair-housed in cages; two pairs and a group of 3 animals were subadult to adult males (aged 4-9 years), and one pair was an adult female with a juvenile male (aged 25 and 1 year respectively). All monkeys were captive born, mother-reared, and housed in the LCE primate facilities at the NIH Animal Center near Poolesville, MD. Breeding groups were housed in one or two parts of three indoor runs (6.9 x 4.1 x 2.1m each), which were connected via sliding doors. Runs were furnished with swings, ladders and various platforms. Cage-housed monkeys were housed in quad cages (1.63 x 1.63 x .71 m per pair). All monkeys were provided with a variety of plastic and metal manipulanda. Monkeys were not food deprived for this study, and received daily nutritional supplements of seeds and fresh fruit or nuts. Commercial monkey biscuits (Labdiet 5045) and water were available *ad libitum*. Further details in Morton et al. (2013).

Comparative Cognition Laboratory, Yale University. Ten monkeys were at the Comparative Cognition Laboratory at Yale University, New Haven, Connecticut, USA. This group consisted of 4 adult males, 4 adult females, and 2 juvenile females. All monkeys were captive born. The monkeys were housed in an indoor enclosure (32 m^3) consisting of multiple compartments. Commercial monkey pellets were provided twice daily (morning, afternoon) and supplemented with fruits, vegetables, nuts, and cereal daily. Water was available *ad libitum*. Further details in Morton et al. (2013).

3.2.2. Personality Ratings

Human Raters. Each subject was rated by one to seven raters (3.24±1.61 raters per monkey). Raters were 25 researchers and 3 care staff, and had at least one year of experience working with their subjects.

Personality Scale. Ratings were made on the Hominoid Personality Questionnaire. A discussion of the history and format of the HPQ was provided in Chapter 2.

Missing Data. Of the 411 questionnaires turned in, 77 were missing between 1 and 28 items (median = 5). In cases where an item was missing, the missing value was replaced with the mean for that item. Excluding questionnaires with missing data for 10 or more items, i.e. those that exceeded the upper end of the 95% confidence interval for amount of missing data, did not yield a different personality structure (Morton et al. 2013). Thus, none of the questionnaires were completely excluded.

3.2.3. Behavioural Measures

Two types of behavioural measures were collected on the 18 capuchins housed at Living Links, UK; there were originally 19 capuchins in the personality study, however one of these subjects died before behavioural data collection commenced. Behavioural data were collected independently of observers' ratings, and were used here to validate interpretations of personality components derived from ratings. The data collection spans the length of a year, during which the Living Links monkeys experienced considerable social changes, including the death of an adult male (East group), ten births (East/West groups), and an on-going shift in dominance between the beta and alpha males (West group; see Loudon 2012).

The first type of behavioural data was collected one year after subjects were rated for personality. Methods of behavioural data collection are provided in Chapter 2; briefly, fifty-four hours of focal observations were recorded over a 4-month sampling period, totalling 3 hours per monkey. Following Martin and Bateson (2007), behaviours and interactions (see Table 2 in Chapter 2) between the focal and other individuals were recorded at 1-min intervals for 10 minutes per day. In addition, in each minute the number of group members within a 2 m radius from the focal monkey was recorded. Subjects were sampled evenly across all periods of the day, usually from 9:00 until 17:30. Incidences of aggression initiated by each monkey were summed across sampling periods; all other behaviours are represented as the percentage of time that individuals spent engaged in each of those behaviours while in view. Aggression data were used to calculate individual differences in monkeys' social rank, i.e. David's scores (see Chapter 2).

The second type of behavioural data was recorded four to seven months after subjects were rated for personality. Fourteen monkeys were filmed and scored on attention span during two learning tasks (see Chapter 2 for details). An illustration of the general setup for each task was provided in Chapter 2. Monkeys' average attention span was scored across each of the three tasks for 24 to 85 randomly selected trials (71.4±23.9 trials per subject). The number of trials selected for each monkey depended on how often they participated during testing (Morton et al. 2013). Attention was assessed on a 3-point scale according to whether they exhibited high ("3"), medium ("2"), or low ("1") attention. High attention was defined as whenever the monkey's head, body, and eyes were directly focused on the task during/between a trial. Medium attention was defined as when a monkey looked away from the task apparatus on one or two occasions during/between a trial. Low attention was defined as when a monkey looked away from the task apparatus on three or more occasions during/between a trial. Monkeys were scored once during a trial, and once again after the trial ended. An overall average attention score was calculated for each monkey across all its trials. Inter-observer reliability tests were conducted using a sub-sample of these data, whereby 120 trials from 5 monkeys were independently scored by two observers, during and after each trial. Cronbach's alpha for each of the five monkeys ranged from 0.70 to 0.90, indicating that each observer's scores were satisfactorily concordant (Field 2009); these results are provided in Table 4. Frequent participants were considered to be more comfortable and motivated to engage in testing (Morton et al. 2013). Thus, in the present analysis, scores on attention span were distinguish between those calculated for all participants (i.e. > 0% average participation), and those calculated specifically for highly consistent participants (i.e. > 75% average participation).

Table 4. Summary of Cronbach's alpha between observers' scores on attention span for five monkeys house at Living Links, UK (N=120 scores/observer). Observers scored each monkey on the same 12 trials, during and after each trial.

Capuchin Monkey	**Cronbach's Alpha**	**Mean Attention Score**	
		Observer 1	**Observer 2**
Junon	0.74	2.75 ± 0.442	2.54 ± 0.658
Carlos	0.862	2.25 ± 0.608	2.17 ± 0.565
Manuel	0.704	1.75 ± 0.608	1.29 ± 0.464
Pedra	0.902	2.42 ± 0.504	2.58 ± 0.504
Sylvie	0.716	2.38 ± 0.5	2.38 ± 0.5

3.2.4. Statistical Analyses

A discussion of the statistics used to analyse personality ratings can be found in Chapter 2. Inter-rater reliabilities, internal consistencies, Everett’s tests, and Procrustes analyses were conducted in collaboration with A. Weiss (University of Edinburgh) using R, version 2.15.2 (R Development Core Team 2012). All other analyses were conducted by F.B. Morton in IBM SPSS Statistics 19. Bonferroni corrections were applied for multiple comparisons involving the same set of variables (Armstrong 2014).

Test-Retest Reliabilities. As discussed in Chapter 2, test-retest reliabilities were examined using Cronbach’s alpha to compare ratings made by each rater over a year from the time they originally filled out the forms. Raters were not informed in advance that they would be asked to re-rate monkeys. Of the original 28 raters that participated in this study, eight (29%) were available to re-rate one monkey each. Five of these raters re-assessed all 54 items; however, one rater reassessed only 50 items, a second rater re-assessed only 41 items, and a third rater re-assessed only 31 items. For raters that rated all 54 items, Cronbach’s alpha values lower than 0.7 were deemed as unreliable (Field 2009). An alpha value of 0.8 was used for raters that re-assessed 41 and 50 items, respectively. An alpha value of 0.9 was used for the rater that re-assessed 31 items. Stricter alpha values were used for raters that did not re-assess all 54 items because 1) the value of alpha depends on the number of items on the scale (Cortina 1993), and 2) it is likely that these raters only rated those items they felt they could comfortably re-assess (thus possibly contributing to alpha inflation).

Cronbach’s alpha for each rater is provided in Table 5. All raters had a Cronbach’s alpha above 0.8, which, as previously discussed, is well above the recommending limit (Field 2009). For raters that re-assessed 41 and 50 items, respectively, alpha values were >0.8, while the rater that rated 31 items had an alpha value of >0.9.

Table 5. Cronbach's alpha values and inter-item correlations for raters that were re-assessed on questionnaires.

Rater	**N Items Re-assessed**	**Cronbach's Alpha**	**Inter-item Correlation**
Rater 1	54	0.867	0.766
Rater 2	54	0.892	0.813
Rater 3	54	0.834	0.754
Rater 4	54	0.887	0.835
Rater 5	54	0.89	0.803
Rater 6	50	0.837	0.77
Rater 7	41	0.882	0.789
Rater 8	31	0.927	0.864

Inter-rater Reliabilities of Items. Of the entire sample across all facilities, 121 capuchins were rated by 2 to 7 raters (4.1±1.7 raters per monkey). As discussed in Chapter 2, two intraclass correlations (ICC [3,1] and ICC[3,k]) were calculated to determine inter-rater reliabilities for subjects rated by at least two raters (Shrout and Fleiss 1979). Following Weiss et al. (2011), any items with inter-rater reliabilities equal to or less than zero were considered unreliable and excluded from further analyses.

The inter-rater reliabilities of all 54 items are presented in Table 9 of the Appendix. The mean $ICC(3,1)$ and $ICC(3,k)$, respectively, of these items were 0.36 (SD = 0.14) and 0.63 (SD = 0.14). The minimum and maximum ICC(3,1), respectively, was 0.12 (*unperceptive*) and 0.75 (*playful*). The minimum and maximum ICC(3,k), respectively, was 0.32 (*unperceptive*) and 0.91

(*playful*). None of the items were unreliable and thus all items were included in the analysis.

Inter-rater Reliabilities and Internal Consistencies of Components. Similar to the item-level analysis, for the 121 subjects rated by at least 2 raters, the inter-rater reliability of components was assessed using Shrout and Fleiss's (1979) *ICC*(3,1) and *ICC*(3,*k*). To determine the internal consistencies, Cronbach's alpha was calculated for each component in the total sample using the alpha function (Revelle 2011). Cronbach's alpha values lower than 0.7 were deemed as unreliable (Field 2009).

Data Reduction. The means across raters were computed for each reliable item. The number of components to extract was determined by examining the scree plot and conducting a parallel analysis (Horn 1965) using the paran function (Dinno 2008). These means were then entered into a principal components analysis (PCA). Components were rotated using both varimax and promax procedures, and loadings ≥ |0.4| were considered to be salient, explaining ~20% of variance (Weiss et al. 2006, 2009, 2011; Field 2009).

Component Interpretation and Validation. Components were interpreted based on the items onto which they loaded and their association with recorded behaviours. Behavioural correlations also served to validate components. Z- scores were calculated for each component (Field 2009); these scores were representative of individual differences in subjects' scores on each personality trait. Pearson correlations were used to test for the associations between component scores and recorded behaviours.

3.3. Results

3.3.3. Data Reduction

The scree plot (Figure 10) suggested that six components should be extracted. Parallel analysis indicated that the eigenvalues of the first six components (14.16, 9.18, 6.80, 3.07, 2.67, and 2.18) were greater than expected under chance at the 95% confidence level (Table 6). However, the last component, which contained loadings from *persistent*, *curious*, *decisive*, and *stable*, only had three loadings greater than or equal to |0.6|, indicating that the component may not be replicable (Guadagnoli and Velicer 1988).

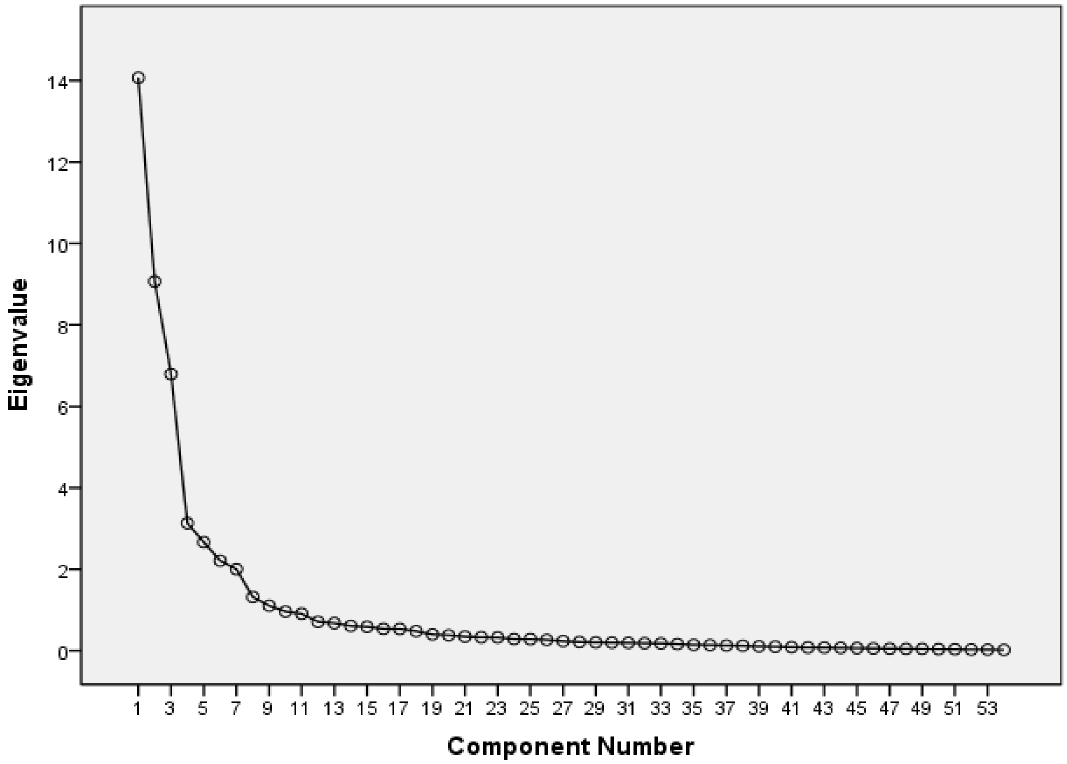


Figure 10. Scree plot from a PCA of the 54 items rated for 127 capuchins.

Table 6. Results of Horn's Parallel Analysis for component retention*.

Component	Adjusted Eigenvalue*	Unadjusted Eigenvalue	Estimated Bias
1	12.430126	14.164260	1.734134
2	7.675491	9.181650	1.506158
3	5.431700	6.804238	1.372538
4	1.814421	3.068727	1.254306
5	1.519686	2.671292	1.151605
6	1.120909	2.180696	1.059787

*Adjusted eigenvalues > 1 indicate dimensions to retain; 1620 iterations, using the 95 percentile estimate.

To determine whether to retain the sixth component, an Everett test (Everett 1988) was conducted. This involved extracting five and six components in samples that excluded one of the sample sites. These five and six component solutions were then compared to the five and six component solutions derived using the full sample by means of targeted orthogonal Procrustes rotations (McCrae et al. 1996). If all six components replicated when dropping individual sites, it could be concluded that the last component is robust and should be retained. If all six components did not replicate, and all five components of the five component solution replicate, it would suggest that only five components should be extracted. When comparing the six component solutions, the last component did not replicate in a sample that did not include subjects from Living Links, USA (Table 7). On the other hand, when comparing the five component solutions, all five components consistently replicated (Table 7). Thus five components were extracted. Varimax and promax rotated six component solutions are available in Table 10 of the Appendix. Correlations among the six promax-rotated components are provided in Table 11 of the Appendix.

Table 7. Everett test of the Robustness of the Six and Five Component Solutions.*

Six Component Solution	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**Congruence**
Bucknell	1.00	0.98	0.98	0.96	0.95	0.98	0.98
Living Links, USA	0.98	0.97	0.96	0.96	0.99	**0.48**	0.93
GSU	1.00	1.00	1.00	.99	1.00	1.00	1.00
Living Links, UK	1.00	1.00	0.99	0.99	0.98	0.99	0.99
NIH	1.00	1.00	1.00	.99	1.00	1.00	1.00
Yale	1.00	1.00	1.00	1.00	.99	1.00	1.00
CNRS	1.00	1.00	1.00	1.00	.99	1.00	1.00

Five Component Solution	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**	**---**	**Congruence**
Bucknell	0.99	0.97	0.94	0.98	0.95	---	0.97
Living Links, USA	0.99	0.99	0.96	0.95	0.95	---	0.97
GSU	1.00	1.00	1.00	1.00	0.99	---	1.00
Living Links, UK	1.00	0.99	0.99	0.98	0.98	---	0.99
NIH	1.00	1.00	0.99	1.00	1.00	---	1.00
Yale	1.00	1.00	1.00	1.00	1.00	---	1.00
CNRS	1.00	1.00	1.00	1.00	1.00	---	1.00

* The site name in each row indicates the site that was left out to generate the loading matrix. The target matrix was either the six or five component varimax-rotated structure based on data from all sites. Components that did not replicate are indicated in boldface. PC = Principal component.

Communalities for the 5-component solution were moderate to high (see Table 12 in Appendix). The varimax- and promax-rotated components were virtually identical (Table 8). Correlations among the promax rotated components were modest (Table 9). Therefore the varimax-rotated components were interpreted, and these results were used for all remaining analyses.

Table 8. Structure Matrix of Varimax- and Promax-Rotated Component Loadings*

	Varimax Rotated Components					**Promax Rotated Components**				
Adjective	**PC1**	**PC2**	**PC3**[a]	**PC4**	**PC5**[a]	**PC1**	**PC2**	**PC3**[a]	**PC4**	**PC5**[a]
Bullying	**0.92**	-0.01	0.14	0.00	-0.03	**0.98**	-0.17	0.12	-0.03	0.02
Aggressive	**0.91**	0.04	0.17	-0.02	-0.04	**0.96**	-0.11	0.15	-0.05	0.02
Submissive	**-0.89**	-0.06	0.10	-0.31	-0.03	**-0.92**	0.12	0.11	-0.30	0.03
Stingy/Greedy	**0.88**	0.08	0.05	0.04	-0.03	**0.90**	-0.06	0.02	0.01	-0.02
Dominant	**0.83**	-0.08	-0.31	-0.05	-0.02	**0.86**	-0.21	-0.35	-0.05	-0.07
Jealous	**0.82**	0.24	0.08	0.02	-0.02	**0.81**	0.12	0.06	-0.03	-0.00
Gentle	**-0.81**	-0.06	**-0.41**	0.06	0.09	**-0.87**	0.07	**-0.40**	0.08	-0.02
Vulnerable	**-0.75**	-0.02	0.14	-0.34	-0.18	**-0.79**	0.15	0.12	-0.30	-0.12
Timid	**-0.68**	**-0.40**	0.19	-0.39	-0.12	**-0.60**	-0.28	0.19	-0.34	-0.01
Irritable	**0.67**	0.02	0.27	-0.32	-0.02	**0.71**	-0.06	0.24	-0.38	0.11
Cautious	**-0.67**	-0.37	-0.01	-0.33	-0.09	**-0.62**	-0.25	-0.01	-0.28	-0.04
Dependent/ Follower	**-0.63**	0.03	**0.41**	0.23	-0.21	**-0.63**	0.11	**0.43**	0.30	-0.19
Independent	**0.61**	0.14	**-0.42**	-0.09	0.01	**0.57**	0.07	**-0.46**	-0.11	-0.07
Manipulative	**0.59**	0.29	0.15	0.39	0.09	**0.56**	0.17	0.17	0.35	0.06
Fearful	**-0.57**	-0.26	0.29	-0.38	-0.29	**-0.52**	-0.14	0.27	-0.31	-0.19
Reckless	**0.53**	**0.49**	0.14	0.06	**-0.46**	**0.44**	**0.45**	0.06	0.12	**-0.50**
Protective	0.37	-0.04	-0.22	0.35	0.30	**0.40**	-0.15	-0.18	0.30	0.23
Inventive	0.11	**0.86**	-0.06	0.18	0.09	-0.10	**0.90**	-0.08	0.09	0.02
Innovative	0.06	**0.85**	-0.03	0.17	0.15	-0.15	**0.89**	-0.03	0.07	0.10
Inquisitive	0.18	**0.83**	0.02	0.33	-0.03	-0.01	**0.84**	0.00	0.28	-0.12
Playful	0.05	**0.76**	0.23	0.35	-0.08	-0.11	**0.78**	0.22	0.32	-0.12
Conventional	-0.13	**-0.73**	-0.31	-0.03	0.19	0.03	**-0.77**	-0.28	0.00	0.17
Active	0.03	**0.72**	**0.45**	0.31	0.17	-0.11	**0.73**	**0.49**	0.20	0.21
Curious	0.11	**0.70**	-0.21	0.00	-0.08	-0.09	**0.75**	-0.26	-0.04	-0.16
Lazy	-0.05	**-0.64**	-0.39	-0.22	-0.37	0.07	**-0.64**	**-0.45**	-0.07	**-0.44**
Imitative	-0.05	**0.63**	0.13	**0.44**	0.07	-0.20	**0.64**	0.15	0.39	0.01
Persistent	0.35	**0.55**	-0.31	-0.21	-0.11	0.19	**0.58**	-0.38	-0.24	-0.17
Defiant	**0.48**	**0.55**	0.18	0.02	-0.21	0.38	**0.51**	0.13	0.00	-0.21
Quitting	-0.01	**-0.50**	0.17	0.04	-0.34	0.13	**-0.54**	0.16	0.17	-0.32
Cool	0.13	0.07	**-0.76**	0.26	0.24	0.07	0.03	**-0.76**	0.23	0.04
Stable	0.00	0.10	**-0.71**	0.01	0.14	-0.08	0.12	**-0.73**	-0.01	-0.02
Excitable	0.04	0.10	**0.64**	-0.10	**-0.48**	0.06	0.11	**0.60**	-0.02	-0.37
Predictable	-0.10	-0.39	**-0.61**	0.08	-0.01	-0.06	**-0.40**	**-0.63**	0.15	-0.15
Unemotional	-0.05	-0.17	**-0.60**	0.32	-0.00	-0.04	-0.20	**-0.61**	0.38	-0.19
Decisive	0.39	0.30	**-0.59**	-0.04	0.24	0.29	0.27	**-0.61**	-0.12	0.13
Impulsive	0.06	**0.40**	**0.59**	-0.13	**-0.45**	0.00	**0.44**	**0.54**	-0.08	-0.35
Sympathetic	-0.39	0.05	**-0.45**	0.38	0.24	**-0.45**	0.08	**-0.42**	0.37	0.09
Sociable	0.15	0.25	-0.16	**0.82**	-0.05	0.10	0.15	-0.14	**0.87**	-0.24
Affectionate	-0.22	0.11	-0.27	**0.74**	-0.00	-0.26	0.07	-0.24	**0.80**	-0.20
Solitary	-0.35	-0.34	0.01	**-0.71**	-0.05	-0.29	-0.23	-0.01	**-0.71**	0.08
Depressed	-0.38	-0.30	0.02	**-0.68**	-0.29	-0.34	-0.18	-0.03	**-0.62**	-0.19
Friendly	-0.37	0.22	-0.21	**0.65**	0.22	**-0.45**	0.22	-0.16	**0.64**	0.07

Anxious	**-0.49**	-0.32	0.25	**-0.55**	-0.27	**-0.43**	-0.20	0.22	**-0.49**	-0.14
Autistic	-0.38	-0.18	0.03	**-0.49**	-0.23	-0.37	-0.07	-0.01	**-0.44**	-0.16
Disorganized	-0.19	0.01	0.20	-0.21	**-0.78**	-0.19	0.08	0.10	-0.03	**-0.78**
Unperceptive	0.06	-0.08	0.17	-0.06	**-0.77**	0.09	-0.08	0.07	0.12	**-0.80**
Thoughtless	-0.05	0.13	0.04	-0.26	**-0.77**	-0.10	0.20	-0.08	-0.09	**-0.81**
Clumsy	-0.18	-0.26	-0.01	0.11	**-0.67**	-0.12	-0.26	-0.09	0.32	**-0.76**
Distractible	0.06	-0.10	**0.43**	0.33	**-0.64**	0.13	-0.16	0.39	**0.51**	**-0.66**
Erratic	0.14	0.23	**0.54**	-0.18	**-0.56**	0.13	0.25	**0.47**	-0.10	**-0.47**
Helpful	-0.25	0.26	-0.37	0.25	**0.41**	-0.35	0.29	-0.32	0.17	0.31
Intelligent	0.07	0.35	-0.23	0.13	0.37	-0.03	0.35	-0.20	0.02	0.32
Sensitive	-0.33	-0.05	-0.30	0.26	0.35	-0.35	-0.04	-0.24	0.22	0.27
Individualistic	-0.06	0.27	-0.08	-0.24	-0.29	-0.15	0.34	-0.14	-0.21	-0.31

*Salient loadings are in boldface. As each component has at least four loadings greater than |.6|, the structure is likely to be stable (Guadagnoli and Velicer 1988). PC=principal component;

[a] Component was reflected by multiplying loadings by -1.

Table 9. Correlations Between Promax Rotated Components.*

Component	PC1	PC2	PC3	PC4
PC2	-0.38	----	----	----
PC3	-0.04	0.00	----	----
PC4	-0.06	0.21	0.12	----
PC5	0.01	-0.10	-0.34	-0.40

*Correlations derived via prior to reflecting Attentiveness and Neuroticism.

3.3.4. Inter-Rater Reliabilities and Internal Consistencies of Components

The inter-rater reliabilities of components were highest for PC1-4; and lowest, though still acceptable, for PC5 (Table 10). The Cronbach’s alpha for PC1-5 were 0.95, 0.92, 0.85, 0.89, and 0.84, respectively.

Table 10. Inter-rater Reliabilities and Capuchin Personality Components.*

Component	***ICC*(3,1)**	***ICC*(3,*k*)**
PC1	0.71	0.89
PC2	0.70	0.89
PC3	0.40	0.69
PC4	0.58	0.82
PC5	0.37	0.67

*Estimates based on 121 capuchin monkeys, each rated by an average of 3.35 raters. *ICC*(3,1) = Reliability of individual ratings. *ICC*(3,*k*) = Reliability of a mean ratings. PC=principal component.

3.3.5. Component Interpretation and Validation

The first component, PC1 (Table 8) was characterized by loadings on items describing high/low aggressive and despotic tendencies (e.g., *bullying*, *aggressive*, *gentle*) (Figure 11). PC1 also had negative loadings for items describing anxiety (e.g., *fearful, cautious*) (Figure 11). PC1 was positively correlated with social rank, the percent of observation time that monkeys were observed aggressing against others, being groomed by others, and negatively correlated with the percentage of observation time that monkeys spent being solitary (see Table 11 and Figure 12). None of the other behavioural categories were significantly related to this component (Table 11). Although none of the significant correlations survived the Bonferroni correction ($P \leq 0.001$), the effect sizes of these correlations were considerably high ($r=|0.56\text{-}0.7|$), explaining between 31.4% and 49% of the total variance. Thus, given these loadings and behavioural correlations, PC1 was labelled “Assertiveness”.

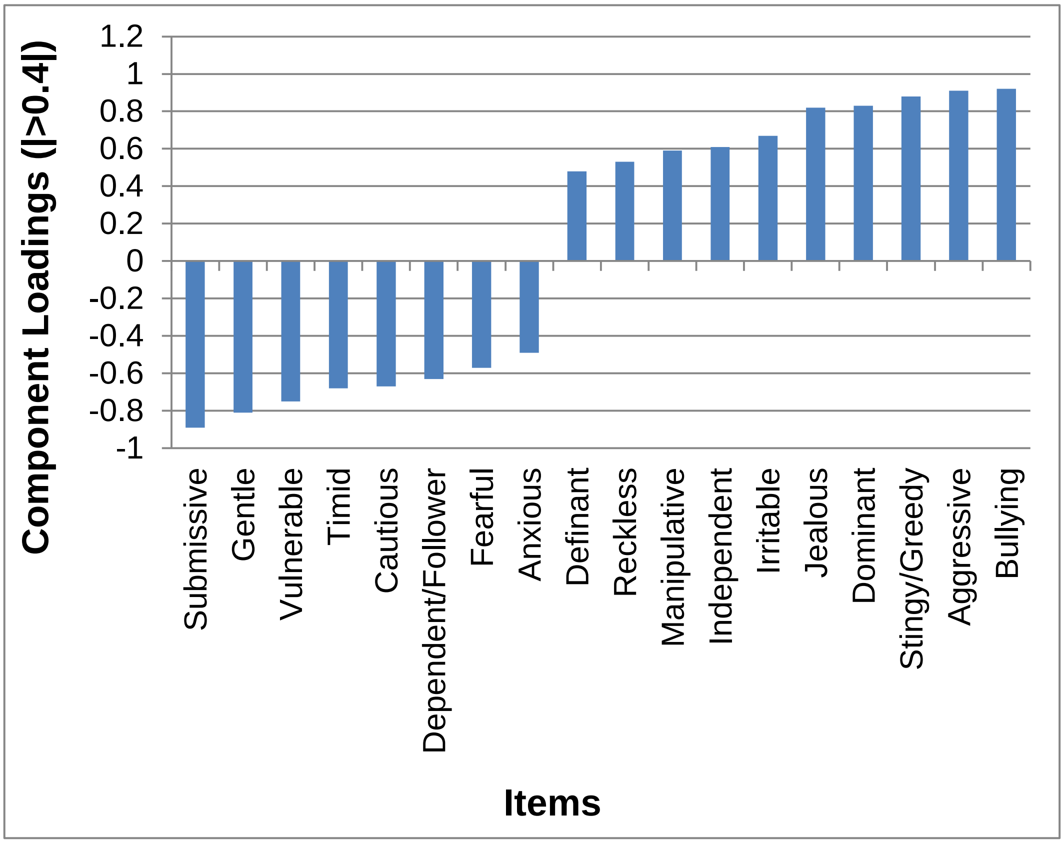


Figure 11. Structure of Assertiveness (only component loadings |>0.4| included). Positive loadings characterize the component more than items with negative loadings.

Table 11. Pearson correlations between personality component scores and behavioural observations at Living Links, UK.

Behaviour	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**
Move[a]	-0.12	-0.02	0.44	-0.45	-0.06
Play[a]	-0.21	0.62**	0.41	0.31	-0.47*
Alert[a]	-0.16	-0.63*	-0.01	-0.58*	0.19
Aggression[a]	0.72**	-0.60**	-0.43	-0.04	0.17
Vigilant[a]	0.09	-0.68**	-0.58*	-0.17	0.58*
Solitary[a]	-0.60**	0.27	0.41	-0.49*	0.06
Attention (all participants)[b]	0.12	0.13	-0.56*	0.30	0.44
Attention (regular participants)[c]	-0.16	-0.19	-0.58	0.25	0.70*
Groomed by others[a]	0.56*	0.17	0.04	0.19	-0.50*
Social rank[a]	0.663**	-0.66**	-0.415	-0.03	0.07

[a] $n = 18$,. [b] $n = 14$. [c] $n = 10$. * $p < 0.05$. ** $p < 0.01$. PC=principal component.

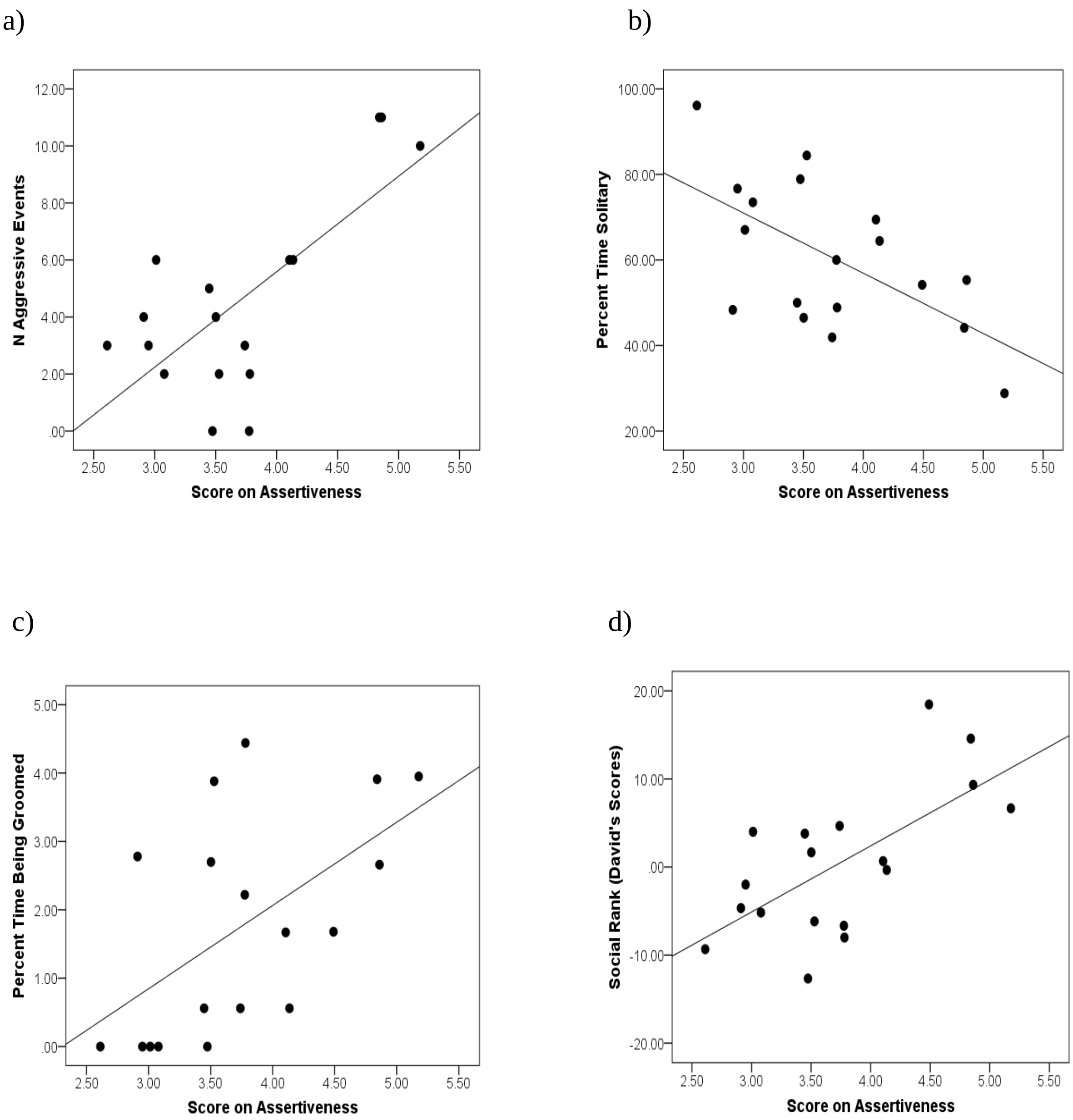


Figure 12. Relationship between Assertiveness and the amount of observation time that monkeys at LL, UK spent a) aggressing towards others, b) solitary, c) being groomed, and d) social rank. Grooming and solitary behaviours are expressed as the percent of time focal individuals were engaged in each behaviour. Incidences of aggression initiated by focal individuals are expressed as the total number of events summed across sampling periods. Social ranks are based on David’s score calculations.

The second component, PC2, (Table 8) was loaded positively by items describing exploratory and investigative behaviour (e.g., *inquisitive*, *curious*), and items associated with creativity and originality (e.g., *inventive*, *innovative*) (Figure 13). PC2 also had positive and negative loadings by items describing high and low energy expenditure, respectively (e.g., *active*, *playful*, *lazy*), and items reflecting a tendency to persevere (e.g. *quitting*, *persistent*) (Figure 13). PC2 was positively correlated with the percentage of time monkeys spent playing and negatively with percentage of time spent being alert, being vigilant, and the total number of occasions monkeys were aggressive towards others (Table 11 and Figure 14). This component was also negatively correlated with scores on social rank (Table 11 and Figure 14). None of the other behavioural categories recorded were significantly related to this component (Table 11). Although none of the significant correlations survived the Bonferroni correction ($P \leq 0.001$), the effect sizes of these correlations were considerably high ($r = |0.6\text{-}0.68|$), explaining between 36% and 46.2% of the total variance. Thus, given the item loadings and behavioural correlates of PC2, the component was labelled “Openness”.

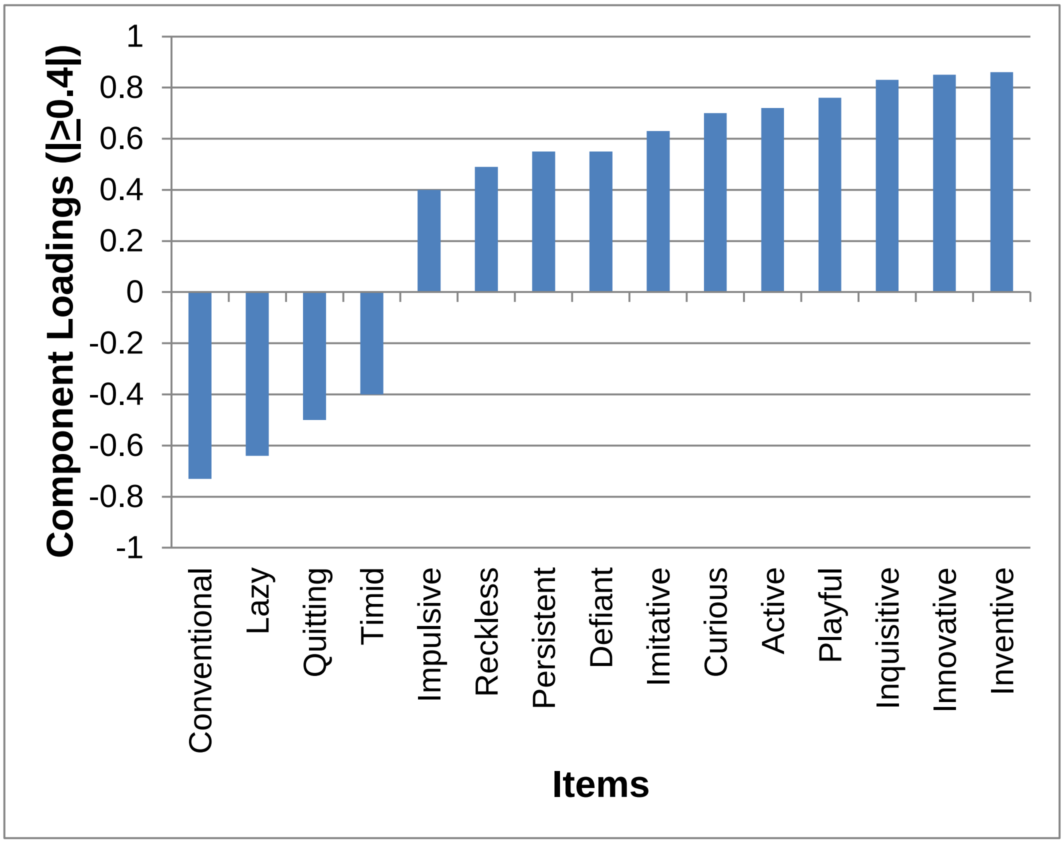
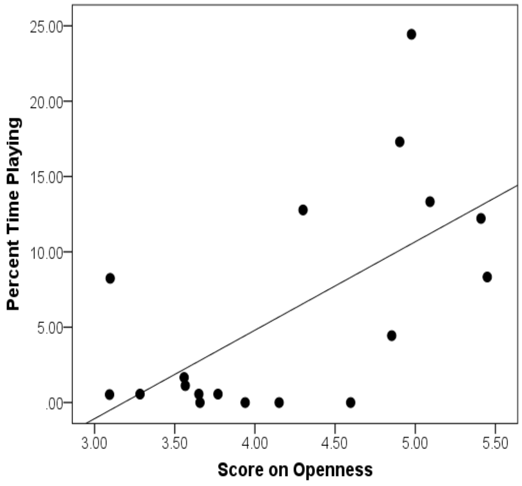
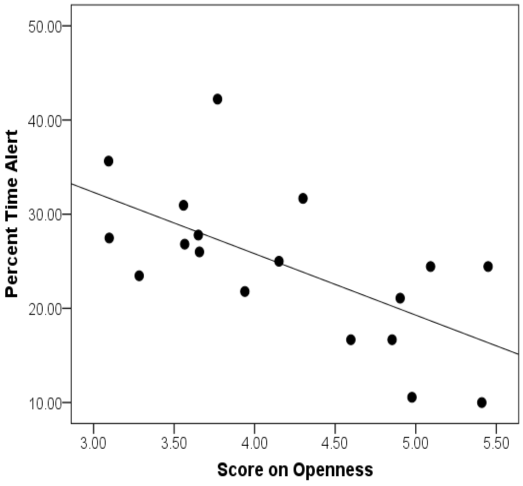


Figure 13. Structure of Openness (only component loadings |>0.4| included). Positive loadings characterize the component more than items with negative loadings.

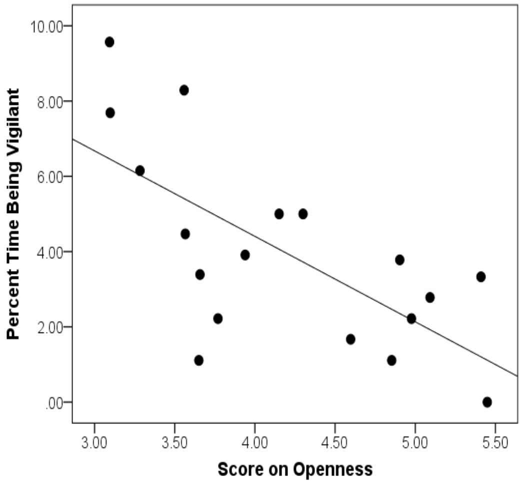
a)


Percent Time Playing
25.00
20.00
15.00
10.00
5.00
.00
3.00
3.50
4.00
4.50
5.00
5.50
Score on Openness

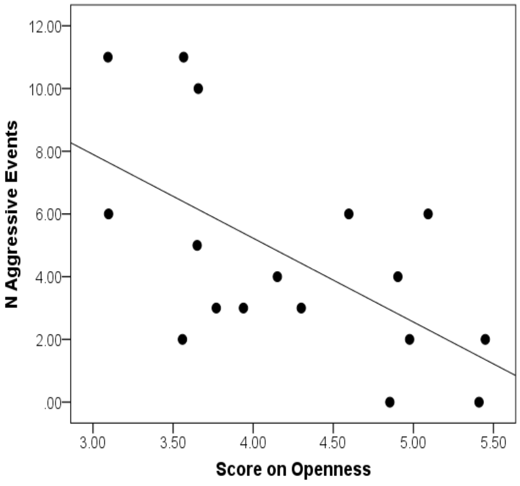
b)


Percent Time Alert
50.00
40.00
30.00
20.00
10.00
3.00
3.50
4.00
4.50
5.00
5.50
Score on Openness

c)


Percent Time Being Vigilant
10.00
8.00
6.00
4.00
2.00
.00
3.00
3.50
4.00
4.50
5.00
5.50
Score on Openness

d)


N Aggressive Events
12.00
10.00
8.00
6.00
4.00
2.00
.00
3.00
3.50
4.00
4.50
5.00
5.50
Score on Openness

e)

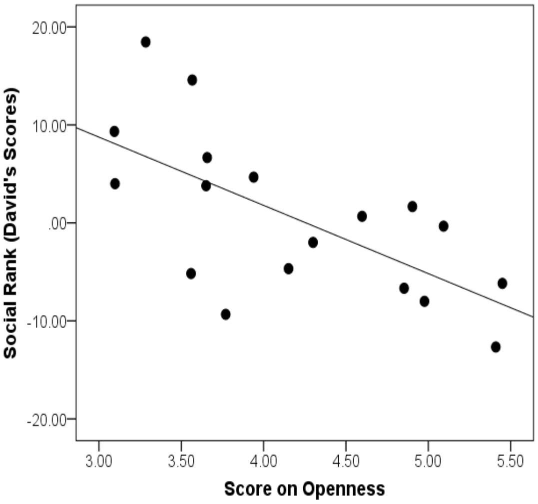


Figure 14. Relationship between Openness and the amount of observation time monkeys at LL, UK spent a) playing, b) alert, c) vigilant, d) aggressing others, and e) social rank. Play, alert, and vigilant behaviours are expressed as the percent of time focal individuals were engaged in each behaviour. Incidences of aggression initiated by focal individuals are expressed as the total number of events summed across sampling periods. Social ranks are based on David's score calculations.

After reflecting the third component, PC3, by multiplying its loadings by -1 (Table 8), it predominantly had positive loadings by items describing an impulsive and volatile disposition (e.g., *excitable*, *impulsive*, *erratic*) (Figure 15). This component also had negative loading by items indicating a calmer disposition (e.g., *cool*, *stable*, *predictable*, *unemotional*) (Figure 15). PC3 was negatively associated with percentage of observation time spent being vigilant, and, among monkeys that participated in testing on learning tasks, attention span (Table 11 and Figure 16). None of the other behaviours were significantly related to this component (Table 11). Although none of the significant correlations survived the Bonferroni correction ($P \leq 0.001$), the effect sizes of these correlations were considerably high (r=|0.56-0.58|), explaining between 31.4% and 33.6% of the total variance. Thus, given the item loadings and associations with behaviours, the component was labelled “Neuroticism”.

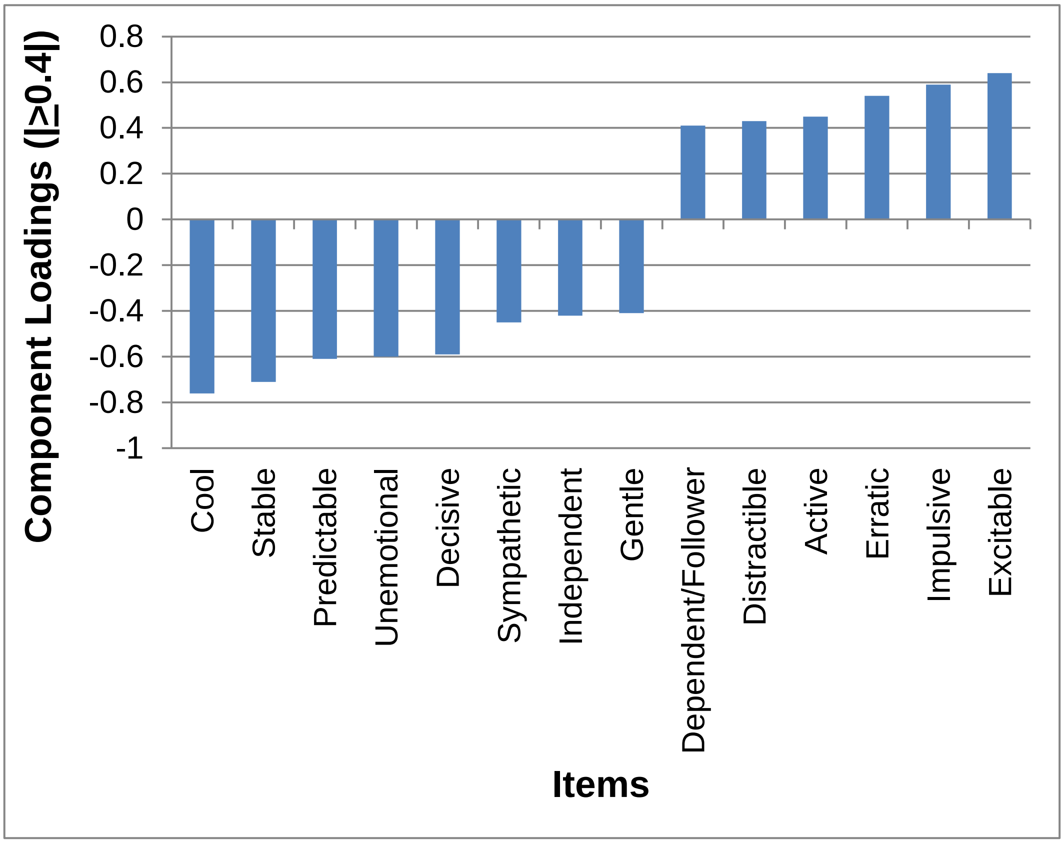


Figure 15. Structure of Neuroticism (only component loadings |>0.4| included). Positive loadings characterize the component more than items with negative loadings.

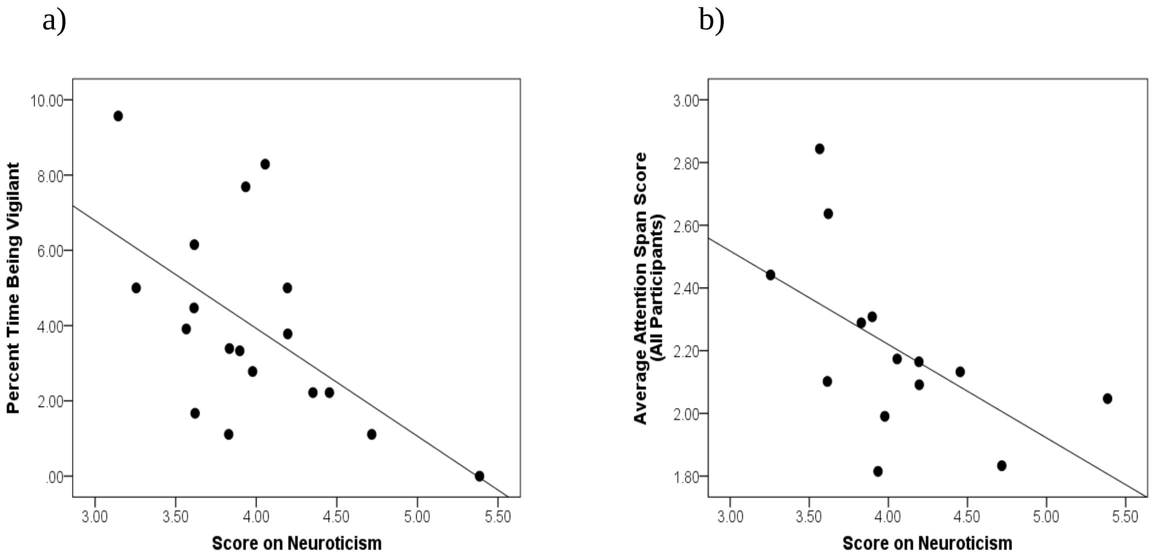


Figure 16. Relationship between Neuroticism and a) the amount of observation time spent vigilant and b) average attention span (all participants) among monkeys at LL, UK. Vigilant behaviour is expressed as the percent of time focal individuals were engaged in this behaviour. Scores on attention span were calculated during learning task sessions according to whether monkeys exhibited high (“3”), medium (“2”), or low (“1”) attention during trials; scores were averaged across trials for each individual.

The fourth component, PC4, (Table 8) had positive and negative loadings from items indicative of overall social embeddedness (e.g., *sociable*, *solitary*) (Figure 17). It also had positive loadings from items describing positive social interactions (e.g., *friendly*, *affectionate*), and negatively on items describing negative affect (e.g., *anxious*, *depressed*) (Figure 17). PC4 was negatively associated with the percentage of time monkeys spent being alert within their main enclosure, as well as time spent alone (Table 11 and Figure 18). None of the other behavioural categories were significantly related to this component (Table 11). Although none of the significant correlations survived the Bonferroni correction ($P \leq 0.001$), the effect sizes of these correlations were reasonably high (r=|0.49-0.58|), explaining between 24% and 33.6% of the total variance. Thus, given the trait loadings and behavioural associations, this component was labelled "Sociability".

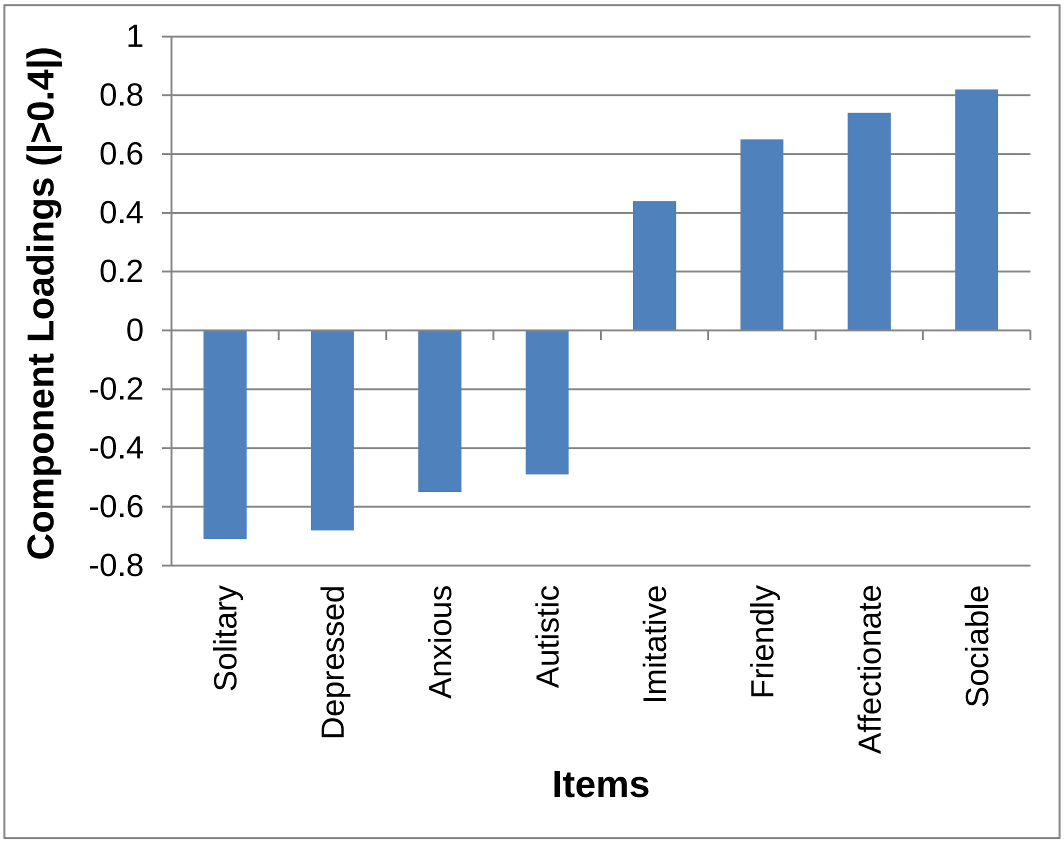


Figure 17. Structure of Sociability (only component loadings |>0.4| included). Positive loadings characterize the component more than items with negative loadings.

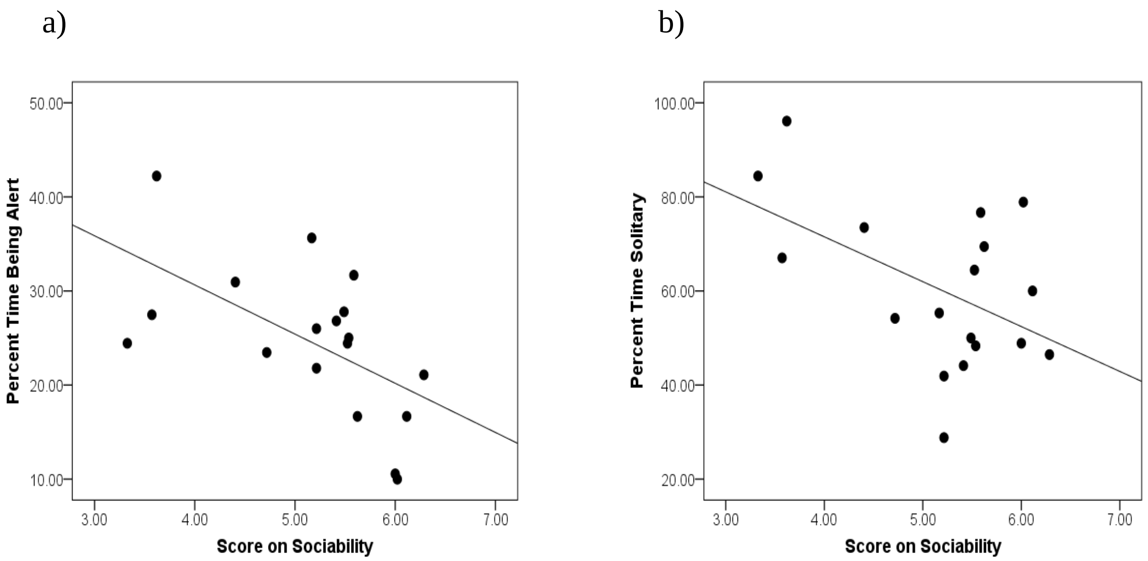


Figure 18. Relationship between Sociability and the amount of observation time monkeys at LL, UK spent a) alert and b) solitary. Alert and solitary behaviours are expressed as the percent of time focal individuals were engaged in each behaviour.

After reflecting the fifth component, PC5 (Table 8), it had negative loadings from items indicating a lack of focus and meticulousness (e.g., *thoughtless*, *distractible*) (Figure 19). This component also had positive and negative loadings, respectively, from items indicating pro-social tendencies and an ability to be discerning (*e.g., helpful*, *unperceptive*) (Figure 19). Scores on PC5 were negatively related to the percentage of time monkeys spent playing and being groomed, and positively with time spent being vigilant (Table 11 and Figure 20). Additionally, among monkeys that participated in over 75% of sessions during testing on learning tasks, scores on PC5 were positively correlated with attention span (Table 11 and Figure 20). None of the other behavioural categories were significantly related to this component (Table 11). Although none of the significant correlations survived the Bonferroni correction ($P \leq 0.001$), the effect sizes of these correlations were moderate to high (r=|0.47-0.7|), explaining between 22.1% and 49% of the total variance. Thus, the item content and behavioural correlations suggests that this component captures facets of the ability to focus one's attention, and therefore this component was labelled "Attentiveness".

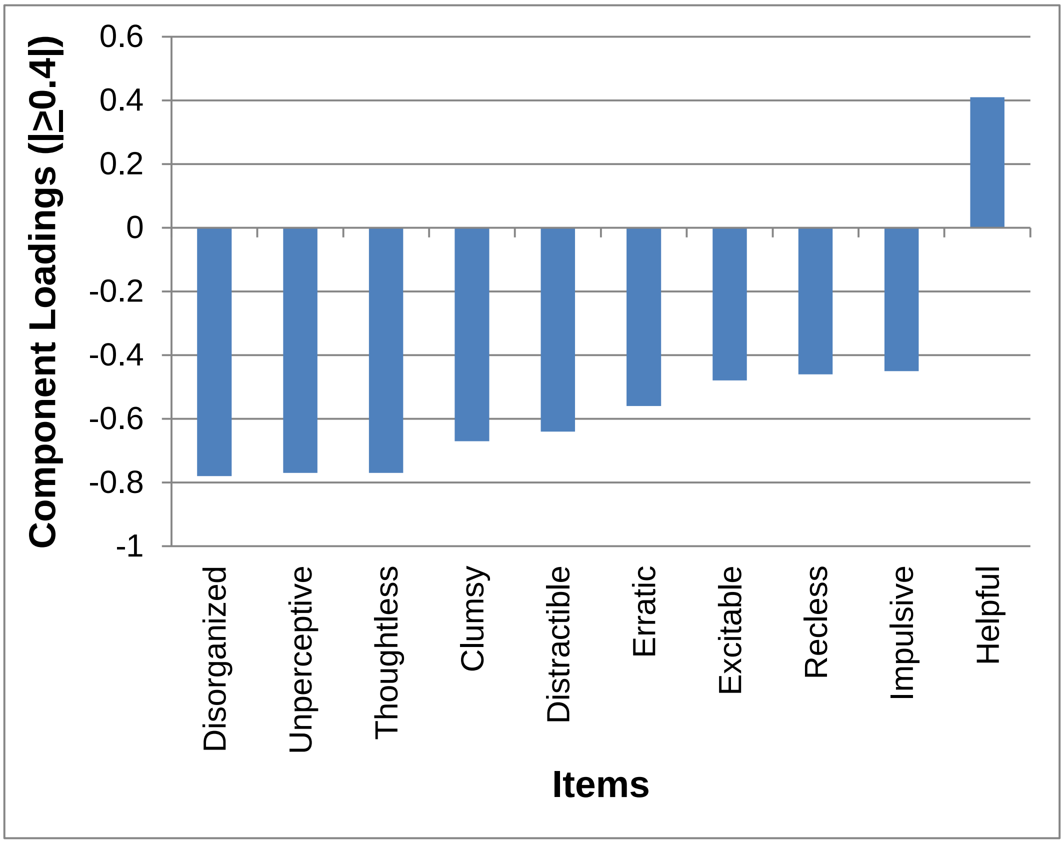


Figure 19. Structure of Attentiveness (only component loadings |>0.4| included). Positive loadings characterize the component more than items with negative loadings.

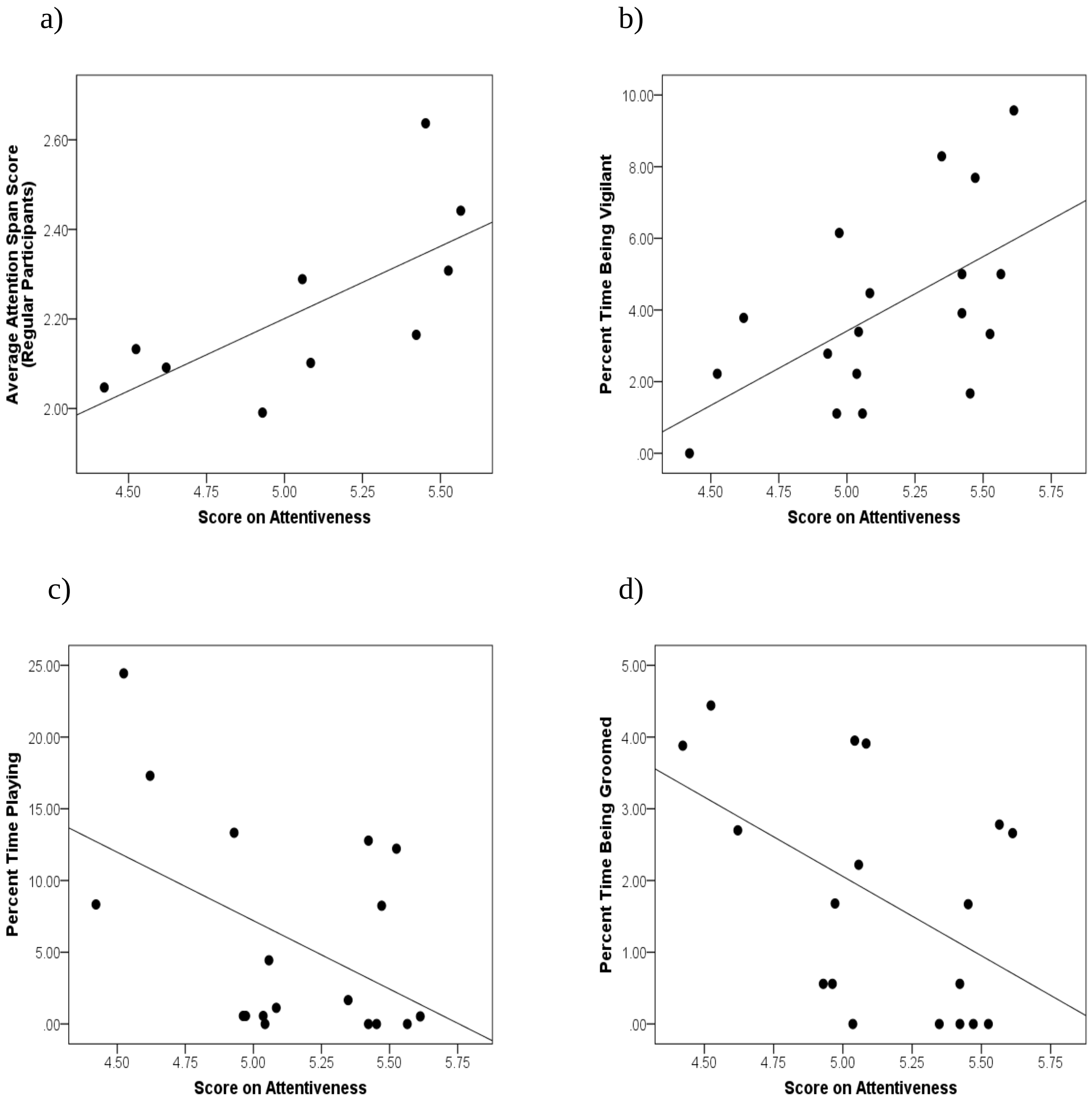


Figure 20. Relationship between scores on Attentiveness and a) average attention span (regular participants) and the amount of observation time monkeys at LL, UK spent b) vigilant, c) playing, and d) being groomed. Play, vigilant, and grooming behaviours are expressed as the percent of time focal individuals were engaged in each behaviour. Scores on attention span were calculated for monkeys that participated on > 75% of learning task sessions, and were scored according to whether participants exhibited high ("3"), medium ("2"), or low ("1") attention during trials; scores were averaged across trials for each individual.

3.4. Discussion

The aims of this study were to investigate personality structure in brown capuchin monkeys, and examine the behavioural validity of individual scores from each dimension. Five robust and behaviourally validated components emerged from a PCA – Assertiveness, Openness, Neuroticism, Sociability, and Attentiveness.

3.4.1. Inter-Rater Reliabilities, Test-Retests, and Internal Consistencies

There was high inter-observer agreement. The ICC's of items were comparable to those in other animal personality studies (Gosling 2001; Uher and Asendorpf 2008; Freeman and Gosling 2010), including those studies that used the same or similar scale as the HPQ (see Table 12). The ICC's were also comparable to those reported in studies of items or lower-order facets of human personality scales (e.g. Kenrick and Stringfield 1980; Costa and McCrae 1992).

Table 12. Inter-observer Reliabilities of Items Reported by Studies Using the HPQ or Similar Scale.

	Item Reliabilities				
Species (N=subjects)	**Mean ICC(3,1)**	**Range ICC(3,1)**	**Mean ICC(3,*k*)**	**Range ICC(3,*k*)**	**N Items**
Barbary macaques * [a] (N=23)	0.40	0.05 (*disorganized*) - 0.85 (*active*)	0.54	0.10 (*disorganized*) - 0.92 (*active*)	45
Barbary macaques ** [a] (N=26)	0.43	0.04 (*unemotional*) - 0.76 (*confident*)	0.58	0.07 (*unemotional*) - 0.86 (*confident*)	49
Brown capuchins [b] (N=127)	0.36	0.12 (*unperceptive*) - 0.75 (*playful*)	0.63	0.32 (*unperceptive*) - 0.91 (*playful*)	54
Chimpanzees [c] (N= 146)	0.28	0.02 (*unemotional*) - 0.58 (*dominant*)	0.54	0.06 (*unemotional*) - 0.82 (*dominant*)	54
Hanuman langurs *** [d] (N=27)	0.31	0.05 (*unemotional*) - 0.77 (*dominant*)	0.58	0.17 (*unemotional*) - 0.93 (*dominant*)	50
Orang-utans [e] (N=152)	0.42	0.2 (predictable) – 0.79 (dominant)	0.64	0.4 (predictable) – 0.91 (dominant)	48
Rhesus macaques [f] (N=125)	0.26	-0.05 (*autistic*) - 0.63 (*dominant*)	0.52	-0.17 (*autistic*) - 0.86 (*dominant*)	54

*Unreliable items excluded: *protective*, *impulsive*, *predictable*, *reckless*, *patient*, *unemotional*; **Unreliable items excluded: *patient*, *reckless*; ***Unreliable items excluded: *persistent*; Three items (*protective*, *predictable*, *selective*) had reliabilities <0.1, but were also excluded; [a] Konečná et al. 2012; [b] this study; [c] Weiss et al. 2009; [d] Konečná et al. 2008; [e] Weiss et al. 2006; [f] Weiss et al. 2007.

Only 29% of the original raters were available for retesting a year after making their original assessments. Among these individuals, there was significant temporal consistency in how individual monkeys were rated on traits. The Chronbach's alpha values calculated for each rater were all above the recommended limit (between 0.7-0.8; Field 2009).

Each component was reliable across raters and internally consistent. The inter-rater reliabilities and internal consistencies of components were comparable to those in studies of primates and other animals (Gosling 2001; Freeman and Gosling 2010), including studies using the same or similar scale as the HPQ (Table 13). Reliabilities of components were also comparable to, if not greater than, those found in studies of human personality (Gomà-i-Freixanet 1997; Gomà-i-Freixanet et al. 2005; Connolly et al. 2007).

Table 13. Inter-rater Reliabilities [ICC(3,1) and ICC(3,*k*)] and Internal Consistencies (α) of Components Reported by Studies Using the HPQ or Similar Scale.

	ICC(3,1)		**ICC(3,*k*)**		**α**		**N Components or Factors**
Species (N=subjects)	**Mean**	**Range**	**Mean**	**Range**	**Mean**	**Range**	
Barbary macaques [a] (N=23)	0.62	0.54 - 0.78	0.76	0.7 - 0.88	0.915	0.91 - 0.92	4
Barbary macaques [a] (N=26)	0.725	0.58 - 0.87	0.835	0.73 - 0.93	0.923	0.89 - 0.95	4
Brown capuchins [b] (N=127)	0.552	0.4 - 0.71	0.792	0.67 - 0.89	0.89	0.84 - 0.95	5
Chimpanzees [c] (N= 146)	0.48	0.32 - 0.63	0.738	0.66 - 0.85	0.832	0.7 - 0.92	6
Chimpanzees [d] (N=100)	0.467	0.33 - 0.64	0.77	0.67 - 0.88	0.876**	0.75-0.94**	6
Chimpanzees [e] (N=74)	0.568	0.43 - 0.76	0.823	0.74 - 0.92	0.887**	0.82-0.93**	6
Chimpanzees [e] (N=43)	0.302	0.17-0.51	0.865	0.77-0.94	0.853**	0.71-0.95**	6
Orang-utans [f] (N=151)	0.618	0.58 - 0.74	0.804	0.73 - 0.88	0.878	0.8 - 0.92	5
Rhesus macaques * [g] (N=124)	0.315	0.1 - 0.45	0.48	0.19 - 0.64	0.865	0.81 - 0.90	6

*Subjects from Wave 1 (see Weiss et al. 2011); ** alphas weighted by number of raters (see King et al. 2005); [a] Konečná et al. 2012; [b] this study; [c] Weiss et al. 2009; [d] King and Figueredo 1997; [e] King et al. 2005; [f] Weiss et al. 2006; [g] Weiss et al. 2007.

3.4.2. Component Interpretation and Validation

Personality has been linked to social rank in various animals, such as fish (Colleter and Brown 2011; Dahlbom et al. 2011), birds (Fox et al. 2009; David et al. 2011), and primates (Anestis 2005; Konečná et al. 2012). Capuchin monkeys typically exhibit a social hierarchy, whereby dominant individuals (the alpha-male and alpha-female) win the majority of conflicts, have preferential access to socioecological resources (e.g. food, coalitions, and mates), and generally are the most socially embedded individuals within groups (Janson 1990; Fragaszy et al. 2004; Tiddi et al. 2011). Moreover, lower-ranking capuchins often receive considerably more aggression from other group members, compared to higher-ranking individuals (e.g. Fragaszy et al. 2004; Ferreira et al. 2006). In this study, Assertiveness reflects some of these “dominant” behaviours in brown capuchins. For instance, within the LL study population, Assertiveness was characterized by positive loadings on items such as *aggressive*, *manipulative*, and *bullying*. Additionally, individual scores on Assertiveness were positively related to the percentage of time that individuals spent being groomed, aggressing towards others, time spent in close proximity (< 2 m) to others, and social rank.

Scores on Openness were positively related to the percentage of time that monkeys spent playing, but negatively related to time monkeys were vigilant, alert, and aggressive towards others. Capuchins are unusual among primates due to their high tolerance of other group members, especially juveniles (Perry 2011). Thus, the negative relationship between Openness and alert/vigilant behaviours could suggest that more open individuals were more socially tolerant and/or less concerned about or distracted by the activities of other group members. In support of this latter suggestion, Byrne and Suomi (2002) found that individual brown capuchins with higher scores on *curious* (a trait that positively loaded onto Openness in this study) had lower levels of cortisol, a hormone associated with arousal and managing stress.

Studies in humans have found that neurotic traits were negatively related to individual differences in attention span – that is, individuals that scored high on these traits were unable to focus as well as individuals that scored low on these traits (Bredemeier et al. 2011). A negative relationship was found here between scores on capuchin Neuroticism and average attention span during testing on learning tasks. During testing, capuchins high in Neuroticism appeared to be easily distracted by on-going activities within the group's main enclosure (e.g., frequently turning to smell or listen for sounds at the cubicle door leading to the group's main enclosure). Scores on Neuroticism were also negatively related to the percentage of time monkeys spent being vigilant. Although this latter finding seems counterintuitive, more neurotic individuals may engage in less vigilant behaviour due to their increased agitation/restlessness. Neuroticism was characterized by traits such as *active*, *excitable*, and *erratic*. Individuals high on Neuroticism also appeared to become more restless when in the presence of other group members, frequently moving out of the way of others and/or continuously circling the main enclosure when others were nearby (pers. obs.).

Scores on Sociability were negatively related to time individuals spent alone. Sociability was negatively related to time monkeys spent alert, i.e. scanning their surroundings. Sociability was characterized by positive loadings on items such as *friendly* and *affectionate*, and negative loadings on items such as *anxious* and *depressed*. Individuals high on Sociability may occupy central positions within their group's social network (see Chapter 6), and as a result, may have been less anxious about the activities and/or whereabouts of other group members. Byrne and Suomi (2002) found that several traits similar to those describing low Sociability (e.g. *apprehensive*, *tense*, *insecure*) were positively related to baseline and peak cortisol levels in brown capuchins. Social Network Analysis provides a clearer picture of how individual differences in Sociability are reflected in differences in monkeys' willingness to affiliate with others (see Chapter 6).

Scores on Attentiveness were negatively related to the percentage of time that individuals spent playing. Such findings mirror those reported by Weinstein and Capitanio (2008), who found a negative relationship between scores on the dimension "Equable" (e.g. *calm* and *easy-going*) and play behaviour in rhesus macaques. Scores on Attentiveness were also positively related to vigilant behaviour. Thus, highly Attentive individuals may have a different status, or role, within the group (e.g. social monitoring or "policing"; see Flack et al. 2006), which was reflected by playing less and being more vigilant. Future studies should examine more closely the association between individual differences in Attentiveness and pro-social behaviour.

Attentiveness was also negatively related to time that monkeys were groomed by others. Among capuchins, this behaviour may alleviate stress and strengthen relationships within the group (Tiddi et al. 2011). Traits such as *erratic*, *excited*, and [not] *helpful* were characteristic of low Attentiveness. Thus, considering the social function of grooming, less Attentive individuals may be groomed more by other members of the group to strengthen relationships between them.

3.4.3. Anthropomorphic Projection?

The PCA results are unlikely to reflect anthropomorphic projection. For instance, Weiss et al. (2012) found that statistically adjusting for rater*item effects (i.e. the linkage between 2 or more items varying as a function of each rater) did not influence the personality structures derived in other primate species (chimpanzees and orang-utans; Weiss et al. 2006, 2009). Within the Living Links, UK sample, scores on each component were related to behaviours recorded up to one year after personality was assessed, suggesting behavioural consistency (i.e. personality) had been measured among the study subjects. More to the point, these latter findings demonstrate that the capuchin ratings do not merely reflect raters' implicit understanding of how personality traits should correlate (in humans).

3.4.4. Future Directions

The present study is not without limitations. For one, the correlations between personality dimensions and behaviours were based on a sample from a single site. Nevertheless, recent studies at the other sites involved in this study have found that the personality scores of their monkeys still predict behavioural patterns >2 years later (e.g. novel object exploration; A. Paukner, pers. comm.). Future research should validate the findings of this study using larger sample sizes and a multi-trait-multi-method approach (Campbell and Fiske 1959).

Another limitation is that the majority of the capuchins at all the different sites used in this study are involved in cognitive research. Thus, their personalities may partly reflect what they learned in these tasks, or the behaviours that were observed while they took part in these tasks. For example, this effect may underlie the clustering of traits found in the sixth component of the PCA (see results in “Data reduction”, and Table 10 in Appendix). Captivity can affect the development and expression of personality (e.g. McDougall et al. 2006). Comparative studies are therefore needed on wild and zoo-housed brown capuchin monkeys (that do not participate in cognitive research) using the same personality scale.

3.5. Conclusions

As discussed in the introduction, studies measuring personality through observer ratings must demonstrate that 1) personality traits rated by observers independently agree with one another, 2) observers are consistent in how they rate individual animals, and 3) scores on personality independently correlate with real-world behaviours in the subjects that were rated. In the present study, personality structure was derived in a large multi-site sample of brown capuchin monkeys. The inter-rater reliabilities of items and the inter-rater reliabilities of components were robust and similar to those in studies of humans and other animals. Raters that were re-assessed on questionnaires for a sub-sample of animals showed strong consistency in their ratings of these individuals across traits. Scores on each of the five personality dimensions were significantly correlated with behaviours recorded across various contexts and up to one year after their personalities were assessed. Thus, the results are consistent with standard definitions of "personality" in animals (Gosling 2001; Carere and Eens 2005), and meet the necessary criteria showing that raters were reliable and valid (Kenrick and Funder 1988; Gosling and Vazire 2002; Freeman and Gosling 2010).

The personality scores derived for individuals in the Living Links, UK sample will be used throughout the remainder of this thesis.

CHAPTER 4

The Structure of Social Relationships in Brown Capuchin Monkeys

Photograph 4

CHAPTER 4

The Structure of Social Relationships in Brown Capuchin Monkeys

4.1. Introduction

Animals form social relationships based on the content, quality, and temporal patterning of their interactions with each other (Hinde 1976). Understanding what factors contribute to variability in these relationships at the species and higher-taxonomic level may contribute to researchers' understanding of the nature and evolution of animal sociality and intelligence (Byrne and Whiten 1988; Shultz and Dunbar 2007). For example, in primates, social grooming is often used to define social relationships between group members (Dunbar 1991; Barrett and Henzi 2001; Lehmann and Dunbar 2009; Tiddi et al. 2011), and species differences in the size of primates' social grooming networks have been shown to positively correlate with species differences in relative brain size (Lehmann and Dunbar 2009), suggesting that larger networks of high-quality relationships are important factors driving the evolution of primate intelligence (Byrne and Whiten 1988; see also Dunbar 1991).

One problem researchers face, however, is how best to quantify social relationships so that these data are comparable between taxa. Although grooming is commonly used to measure social relationships among primates, this behaviour may not serve the same social function for all animals (e.g. basic hygienic purposes; Clayton et al. 2010), thereby making it a difficult measure to use in comparative studies across taxa. Similarly, while spatial proximity has been proposed as a suitable measure of animals' social relationships (i.e. since animals within close proximity are more likely to interact with each other; Whitehead 2008), not all authors agree. For instance, animals may come within close proximity to each other due to localized habitat preferences, but never actually interact with one another (discussed in Wey et al. 2008). One way that proximity has been used to assess relationship quality is through network analyses (see Chapter 6). In cases where spatial proximity reflects the likelihood of interactions occurring between individuals, there are nevertheless important species differences in terms of the content and quality of interactions that spatial proximity associations might capture (e.g. food sharing, mating, play, inspecting infants, or physical conflict; Whitehead 2008). Another issue that researchers face is how to define the "quality" of a social relationship. Traditionally, social relationship quality has been defined in terms of afflilative (e.g. tolerance) and agonistic behaviour (e.g. conflict), whereby dyads that engage in affiliative acts more than agonistic acts are considered to share a higher-quality relationship with one another (Cords and Aureli 2000; Natoli et al. 2001; Weaver et al. 2004; Lea et al. 2010). However, Cords and Aureli (2000) proposed that social relationship quality could be defined in terms of three components: 1) value (i.e. immediate benefits afforded by the relationship, such as grooming), 2) compatibility (i.e. tolerance based on partners' shared history), and 3) security (i.e. consistency and predictability in partners' behaviour, like rates of aggression).

Data reduction techniques, such as factor analysis (FA) or principal components analysis (PCA), have proven to be useful tools for addressing the issues outline above since such methods can identify inter-relationships between a set of potentially correlated variables, and cluster correlated behaviours into fewer discrete categories called "factors" or "components", respectively (Field 2009). PCA is increasingly being used by researchers to describe the social relationships of animals, such as rhesus macaques (Simpson and Howe 1980; Manson 1997), Japanese macaques (Schino et al. 1995; Soltis 1999; Majolo et al. 2010), Barbary macaques (McFarland and Majolo 2011), spider monkeys (*Ateles geoffroyi*; Rebeccini et al. 2011), chimpanzees (Fraser et al. 2008; Koski et al. 2012), and common ravens (*Corvus corax*; Fraser and Bugnyar 2010; Loretto et al. 2012). With the exception of Rebechini et al. (2011), these studies have largely supported the 3-component model of social relationship structure (i.e. how many components exist and what behaviours characterise them) as proposed by Cords and Aureli (2000). A cross all of these studies, time spent in close spatial proximity with others has consistently loaded onto a component reflecting relationship “value”, indicating that this behaviour may serve as a reliable proxy for relationship value in comparative studies. Comparisons across these studies also find that behaviours do not load consistently onto the same components. For example, some studies have reported that rates of aggression load onto a component reflecting relationship “compatibility” (Fraser et al. 2008; Fraser and Bugnyar 2010; McFarland and Majolo 2011), whereas other studies have found that this behaviour loads onto a component reflecting relationship “security” (Majolo et al. 2010; see also the component labelled “risk” in Rebeccini et al. 2011). Such findings illustrate how PCA can be useful for identifying what behaviours may be suitable for measuring and comparing social relationships across taxa.

4.1.2. Methodological Considerations for Data Reduction in Relationship Studies

When subjecting one’s data to a data reduction analysis, it is necessary for the research to instruct the server how many factors or components to extract from the analysis (Field 2009). This decision is critical given that it will influence how variables cluster onto factors/components, thereby affecting the final solution (and hence) researchers’ interpretation of those results (Zwick and Velicer 1986; Ledesma and Valero-Mora 2007). Under-extraction may result in the loss of relevant information and can distort the overall solution, whereas over-extraction may result in some factors or components being unstable and thus difficult to interpret and/or replicate (Zwick and Velicer 1986).

Deciding when to stop extracting factors or components depends on when very little “random” variability remains in the final solution. Various “cut-offs” have been developed to help researchers make this decision, which involve calculating the amount of variation that is explained by each factor/component (called “eigenvalues”; Field 2009). Two commonly used methods are Kaiser’s criterion and scree tests. Kaiser’s criterion retains components with eigenvalues >1.0; meaning, each component accounts for more variance than what is accounted by one of the original variables (Kaiser 1960). Scree tests are a graphical technique that plots eigenvalues in a simple line plot. The number of factors/components to extract are visually estimated from the scree plot by finding the point where the line begins to level off; all components to the right of this point are considered random “noise” and should therefore not be retained (Cattell 1966). The problem with using either Kaiser’s criterion or scree tests is that although each of these techniques are relatively simple to perform (thus contributing to their common usage by researchers), they can often lead to spurious solutions. In particular, Kaiser’s criterion has a tendency to overestimate the number of factors/components that should be extracted, while scree plots are subjective and sometimes may lead to under- or over-estimation particularly as the line of the plot begins to asymptote (Zwick and Velicer 1986). Collectively, using these techniques to determine factor/component extraction is not recommended by most statisticians (Zwick and Velicer 1986; Ledesma and Valero-Mora 2007). In light of these deficiencies, an alternative method commonly recommended by statisticians is Horn’s (1965) parallel analysis (PA). This procedure is considered by many to be the least subjective of all methods for extraction given that it is based on generating random eigenvalues that “parallel” the observed data in terms of sample size and the number of variables (Zwick and Valicer 1986); a factor or component is retained if its eigenvalue is greater than the 95th percentile of the distribution of eigenvalues generated from the random data (Horn 1965).

To date, all studies using data reduction to describe the social relationships of animals have used Kaiser's criterion to determine the number of components to extract, and one of these studies (Koski et al. 2012) supplemented this with a scree test. It remains unclear to what extent these methods affect one's interpretations of the final solution. To investigate this question further, PCA was used to characterize the social relationships of two captive groups of brown capuchin monkeys housed at the "Living Links to Human Evolution" Research Centre, UK. Ten affiliative and agonistic behaviours were recorded among social partners in both groups (Chapter 2). Three methods were used to determine the number of components to retain in the analysis, including Kaiser's criterion, a scree test, and parallel analysis. The final results of the PCA were compared according to which component extraction method was used.

4.2. Methods and Materials

4.2.1. Behavioural Sampling

Two sets of behavioural data were obtained. In the first set, fifty-four hours of focal observations were recorded, totalling 3 hours per individual. The second set of behavioural data was based on subjects' approaches to one another at a cluster of five puzzle feeders; all instances were recorded in which a monkey approached another monkey at a feeding site, noting whether the receiving monkey responded to their approach by either avoiding or staying at the feeder. These data were used to calculate avoid-stay symmetries (see Section 4.2.3.). Details for all behavioural methods are provided in Chapter 2.

A total of 3,240 focal minutes of observation were collected on each member of East and West group, of which 888 minutes consisted of monkeys within close spatial proximity to each focal (excluding grooming and social foraging), 346 focal minutes consisted of social foraging, and 133 minutes consisted of social grooming. Additionally, monkeys engaged in a total of 32 food sharing events, 74 conflicts, and 15 coalitions. Finally, during the outdoor puzzle feeder experiments, a total of 795 approaches/avoidances were recorded. Means per dyad for each social behaviour are provided in Table 14; the raw data for each dyad are provided in Table 4 of the Appendix.

Table 14. Mean (±SE) social behaviour per monkey dyad (N=73 dyads).

Social Behaviour	**Mean (±SE) per Dyad**
Avoid/Stay Symmetry	-7.32 ± 1.302*
Coalitions	0.21 ±0.07
Conflict	1.01 ± 0.177
Conflict Symmetry	0.49 ± 0.186
Food Sharing	0.44 ± 0.107
Food Sharing Symmetry	0.001 ± 0.098
Grooming	1.82 ± 0.413
Grooming Symmetry	0.03 ± 0.346
Spatial Proximity	12.16 ± 1.632
Social Foraging	4.74 ± 0.639

*Negative value indicates the first monkey within the dyad stayed more than avoided when approached by the other monkey.

4.2.2. Behavioural Calculations

Following previous studies (e.g. Rebecchini et al. 2011; Koski et al. 2012), the following calculations were made using the behaviours recorded in East and West groups (Tables 15 and

16), resulting in a total of 73 dyads. These calculations, which are provided in Table 4 of the Appendix, were subjected to a principal components analysis (see Section 4.2.4.).

Table 15. Social behaviours entered into a principal components analysis.

Social Behaviour	**Definition**
Avoid/Stay Symmetry	Symmetry in the number of times a monkey avoided/stayed at a monopolizeable food source as they were approached by the other member of the dyad.
Coalitions	Number of aggressive events in which one member of the dyad supports the other.
Conflict	Number of aggressive events within the dyad.
Conflict Symmetry	Symmetry in conflict within the dyad.
Food Sharing	Number of food sharing events within the dyad.
Food Sharing Symmetry	Symmetry in food sharing within the dyad.
Grooming	Number of focal minutes spent grooming each other.
Grooming Symmetry	Symmetry in grooming within the dyad.
Social Foraging	Number of focal minutes spent in close proximity ($\leq$2 body lengths) from each other while at least one member of the dyad is engaged in foraging.
Spatial Proximity	Number of focal minutes spent in close proximity ($\leq$2 body lengths) from each other.

Table 16. Behavioural measures calculated for each social dyad.*

Social Behavior	**Calculation**
Avoid/Stay Symmetry	(# times A approaches B) / [(# times A approaches B) + (# times B approaches A)]
Coalitions	[(# times A supports B) + (# times B supports A)]
Conflict	[(# times A aggresses B) + (# times B aggresses A)]
Conflict Symmetry	(# times A aggresses B) / [(# times A aggresses B) + (# times B aggresses A)]
Food Sharing	[(# times A gives to B) + (# times B gives to A)]
Food Sharing Symmetry	(# times A gives to B / [(# times A gives to B) + (# times B gives to A)]
Grooming	[(# minutes A grooms B) + (# minutes B grooms A)]
Grooming Symmetry	(# minutes A grooms B) / [(# minutes A grooms B) + (# minutes B grooms A)]
Social Foraging	[(% of time A within proximity of B) + (% of time B within proximity of A)]
Spatial Proximity	[(% of time A within proximity of B) + (% of time B within proximity of A)]**

*Modified from Rebecchini et al. (2011) and Koski et al. (2012). **These calculations do not include time spent grooming or time spent social foraging.

4.2.3. Statistical Analyses

PCA was used to examine social relationship structure; missing values were replaced with the mean of that column (Field 2009). PCA, Kaiser's criterion, and the scree test were conducted by F.B. M. in IBM SPSS Statistics 19. Parallel analysis was conducted in collaboration with Alexander Weiss (University of Edinburgh) using the paran function (Dinno 2008) available in R (version 3.0.1.). In the final PCA solution, loadings greater than |0.4| were considered salient (Koski et al. 2012). Components with high loadings (i.e. |0.7|) and/or those with four or more loadings greater than |0.4| were considered robust (Guadagnoli and Velicer 1988; Field 2009).

4.3. Results

4.3.1. PCA Using Kaiser's Criterion

Three components had eigenvalues over Kaiser's criterion of 1.0, and explained 67.32% of the total variance. The first component was moderately correlated with the second component (r=0.493), and weakly correlated with the third component (r=-0.106) (Table 17). The second component was weakly correlated with the third component (r=0.01; Table 17). Communalities for the 3-component solution were moderate to high (Table 13 in Appendix). The varimax- and promax-rotated solutions revealed little difference in structure (Table 18). Thus, interpretations of component structure were based on the varimax-rotated solution.

Table 17. Correlation matrix between components (Promax rotation).

Component	1	2	3
1	1.000	.493	-.106
2	.493	1.000	.010
3	-.106	.010	1.000

Table 18. Varimax- and promax-rotated structures.*

Behavioural Calculation	Varimax Rotation			Promax Rotation		
	PC1	PC2	PC3	PC1	PC2	PC3
Spatial Proximity	**.863**	.274	.028	**.887**	.044	.075
Grooming	**.806**	.285	.050	**.822**	.073	.092
Grooming Symmetry	**-.743**	.099	.168	**-.850**	.329	.119
Avoid/Stay Symmetry	.048	**-.763**	-.036	.275	**-.862**	-.010
Food Sharing	.247	**.680**	-.202	.064	**.688**	-.207
Food Sharing Symmetry	.088	**.658**	.175	-.082	**.700**	.162
Coalitions	**.434**	**.658**	-.064	.288	**.604**	-.056
Social Foraging	**.590**	**.607**	-.011	**.482**	**.498**	.009
Conflict Symmetry	.006	.033	**.899**	.060	.006	**.904**
Conflict	-.086	-.019	**.898**	-.029	-.023	**.899**

*Salient loadings (>|0.4|) per behaviour are in bold; PC=principal component.

Component 1 had an eigenvalue of 2.56 and explained 25.6% of the variance. This component (Table 18) was characterized by moderate to high loadings (>0.4) on behaviours indicating the importance of the relationship in terms of social affiliation (i.e. proximity, social foraging) and direct benefits gained from this affiliation (i.e. grooming, grooming symmetry, coalitions). The component was therefore labelled “value” following the definition of relationship value in Cords and Aureli (2000).

Component 2 had an eigenvalue of 2.45 and explained 24.48% of the variance. This component (Table 18) was characterized by moderate to high loadings (>0.4) from behaviours related to tolerance to approaches (avoid-stay symmetry), tolerance at feeding sites (social foraging, food sharing, food sharing symmetry), and coalitionary support. This component was therefore labelled “compatibility” as it approximated the definition of relationship compatibility as defined by Cords and Aureli (2000).

Component 3 had an eigenvector of 1.72 and explained 17.24% of the variance. This component (Table 18) was characterized by high loadings (>0.89) from behaviours indicating a lack of stability or predictability in the relationship (i.e. conflict and conflict symmetry), which reflected "security" as defined by Cords and Aureli (2000) and was therefore labelled as such.

4.3.2. PCA Using Scree Test and Parallel Analysis

Both the scree plot (Figure 21) and results of the parallel analysis (Table 19) suggested that only two components should be retained in the final PCA solution. Collectively, these components explained 55.0% of the total variance, and were weakly correlated (r=-0.072). Communalities for the 2-component solution were moderate to high (Table 14 in Appendix). Components were minimally correlated (Table 20). A comparison between the varimax- and promax-rotated solutions revealed little difference in structure (Table 21). Thus, interpretations of component structure were based on the varimax-rotated solution.

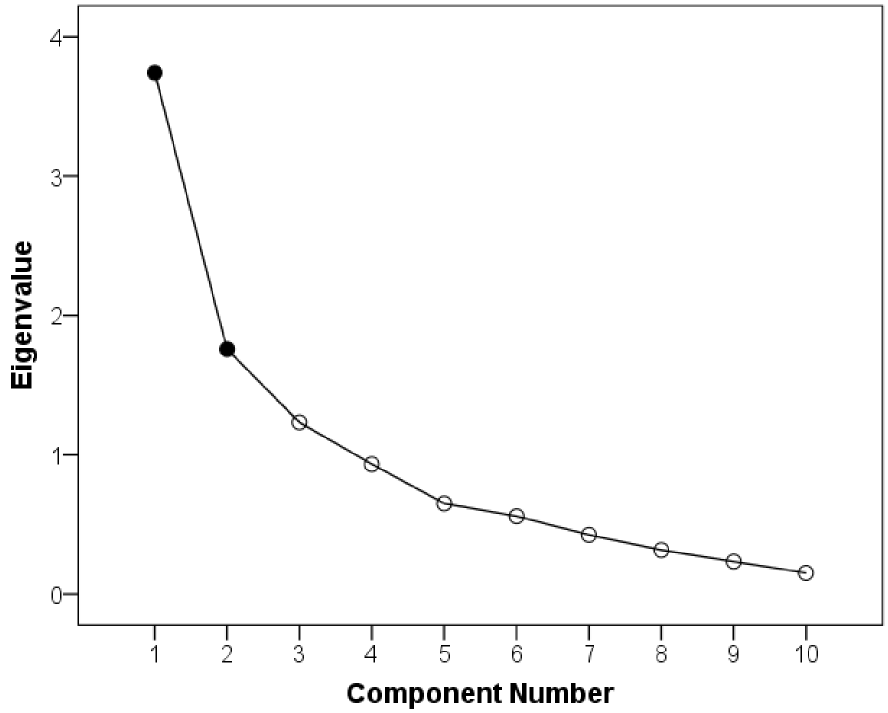


Figure 21. Scree Test for Component Retention. Black circles indicate components that were retained; clear circles indicate components that were discarded.

Table 19. Results of Horn's (1965) Parallel Analysis for Component Retention.*

Component	**Adjusted Eigenvalues**
1	**2.920683**
2	**1.202033**
3	0.858408
4	0.708558
5	0.549795
6	0.568731
7	0.533918
8	0.527448
9	0.549315
10	0.568179

*1,000 iterations, using the 95th percentile estimate; adjusted eigenvalues >1.0 indicate dimensions to retain; 2 components retained (boldface).

Unadjusted eigenvalues are also those used for the scree test in Figure 21.

Table 20. Correlation matrix between components (Promax rotation)

Component	1	2
1	1.000	-.072
2	-.072	1.000

Table 21. Varimax- and promax-rotated structures.*

Behavioural Calculation	Varimax Rotation		Promax Rotation	
	PC1	PC2	PC1	PC2
Spatial Proximity	**.803**	-.112	**.802**	-.078
Grooming	**.772**	-.077	**.771**	-.044
Grooming Symmetry	**-.450**	.343	**-.441**	.325
Avoid/Stay Symmetry	**-.507**	-.188	**-.514**	-.210
Food Sharing	**.651**	-.120	**.649**	-.092
Food Sharing Symmetry	**.532**	.272	**.541**	.295
Coalitions	**.771**	-.033	**.771**	.000
Social Foraging	**.846**	-.026	**.847**	.010
Conflict Symmetry	.049	**.865**	.075	**.869**
Conflict	-.053	**.875**	-.027	**.875**

*Salient loadings (>|0.4|) for each behaviour are highlighted in bold; PC=principal component.

Component 1 had an eigenvalue of 3.72 and explained 37.22% of the variance. This component was characterized by moderate to high loadings ($\geq$|0.45|) on behaviours related to social affiliation (e.g. proximity, social foraging, food sharing, and grooming). The component was therefore labelled “affiliative”.

Component 2 had an eigenvalue of 1.78 and explained 17.8% of the variance. This component was characterized by high loadings ($\geq$|0.869|) from agonistic behaviours, i.e. conflict and conflict symmetry. The component was therefore labelled “agonistic”.

4.4. Discussion

The present study compared the results of a PCA of ten behavioural measures using three methods of component retention (Kaiser's criterion, scree tests, and parallel analysis) to determine how best to define the social relationships of brown capuchin monkeys. Based on Kaiser's criterion, three components were retained, and the loadings of these components resembled the 3-component model proposed by Cords and Aureli (2000), i.e. relationship value (e.g. grooming and food sharing), compatibility (e.g. tolerance at feeding sites), and security (e.g. rates of aggression). Examining the individual loadings of this PCA solution and comparing them with those reported in previous studies, important differences appeared to exist across species. In particular, in capuchins and Japanese macaques, aggression loaded positively onto a component resembling relationship "security" (this study; Majolo et al. 2010), whereas in chimpanzees, Barbary macaques, and corvids, this behaviour loaded positively onto a component resembling relationship "compatibility" (Fraser et al. 2008; Fraser and Bugnyar 2010; Koski et al. 2012). Similarly, in capuchins and Japanese macaques (this study; Majolo et al. 2010), grooming symmetry loaded positively onto a component resembling relationship "value", whereas in chimpanzees and Barbary macaques, this behaviour loaded positively onto a component resembling relationship "security" (Fraser et al. 2008; McFarland and Majolo 2011).

Two possible explanations may underlie these results. First, such findings could indicate that aggression and grooming symmetry have different meanings in terms of the social relationships of capuchins and Barbary macaques compared to other species. Alternatively, such findings could simply reflect instability in the PCA solutions. For instance, according to Guadagnoli and Velicer (1988) components with high loadings (i.e. |0.7|) and/or those with four or more loadings greater than |0.4| should be considered robust, yet not all of the aforementioned studies report components that meet these requirements (e.g. relationship “security” in chimpanzees; Fraser et al. 2008). However, because the Kaiser’s criterion was the only method used in previous studies, it is impossible to differentiate between these two possibilities at present.

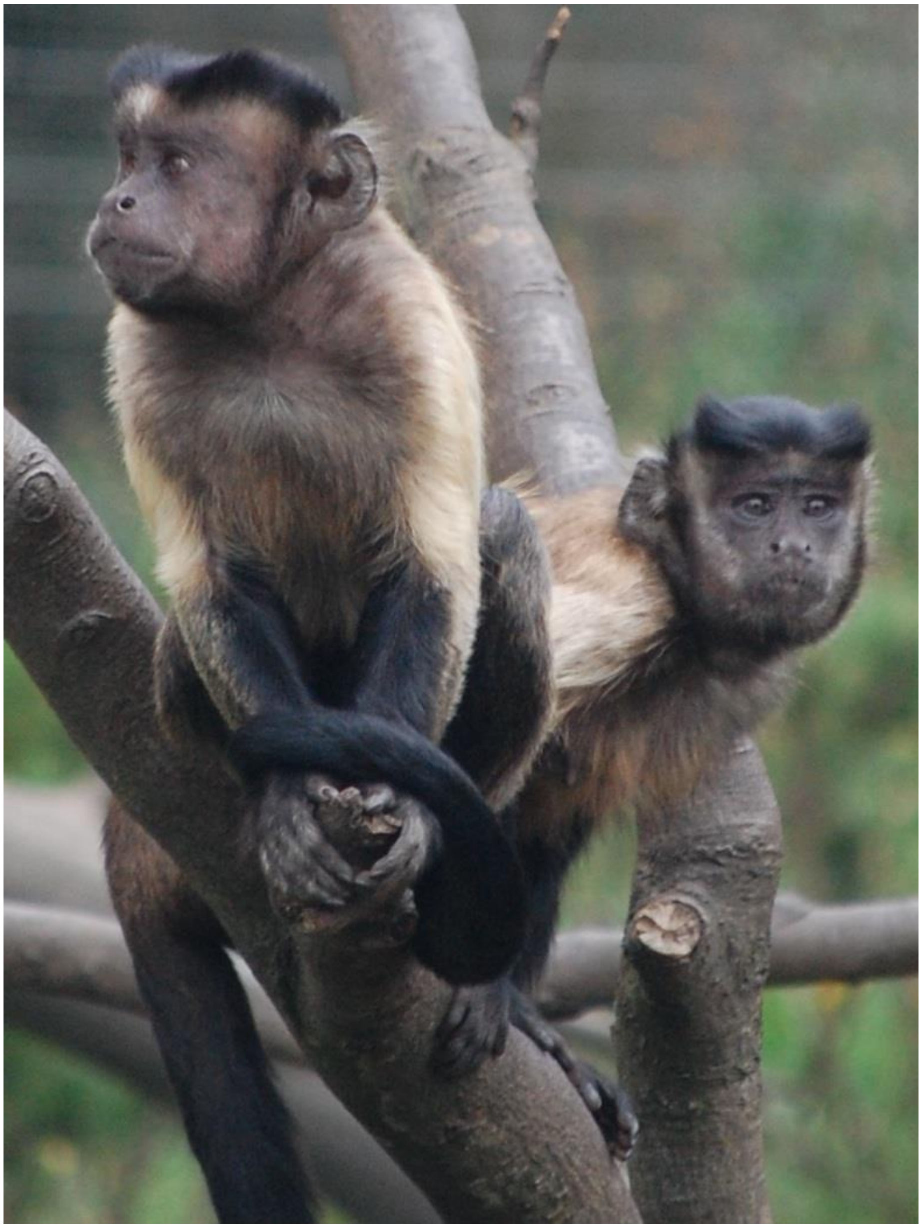
In contrast to the PCA solution derived using Kaiser’s criterion, both the scree plot and parallel analysis indicated that only two components should be retained, resulting in all behaviours loading onto either an “affiliative” and “agonistic” component. Compared to the 3-component solution, correlations between components were only weakly correlated. Therefore, according to this latter solution, capuchin social relationships are best described in terms of their affiliative and agonistic content, which does not support the existence of a 3-component model for social relationships in this species (Cords and Aureli 2000). Additionally, behaviours such as grooming and tolerance at feeding sites, which loaded onto different components in the Kaiser-based solution (see Table 18), are likely to have similar meanings in terms of social function because here they loaded onto the *same* component.

4.5. Conclusions

This study illustrates the importance of making careful decisions regarding how many components (or factors) to retain from data reduction analyses. Doing so may lead to a better and more systematic understanding of how best to define and measure social relationships among animals, which in turn can facilitate comparative studies of sociality. As a further cautionary note, however, although this study emphasizes using parallel analysis because it provides a less subjective method for component extraction (Horn 1979; Zwick and Velicer 1986), this does not necessarily mean that it is “more reliable” *per se*. In Chapter 3, a parallel analysis suggested that six components should be retained from a PCA of 54 items from 127 subjects, whereas in contrast, a scree plot suggested that only five should be retained. In such cases, further analysis such as an Everett's test (Everett 1988) may be required to make an informed decision regarding component extraction. However, in the present study, because the parallel analysis and scree test both suggested two components should be extracted, and these components were weakly correlated compared to the 3-component solution, the 2-component model will be used throughout the remainder of this thesis.

CHAPTER 5

Factors Affecting Social Relationship Quality in Brown Capuchin Monkeys



Photograph 5

CHAPTER 5

Factors Affecting Social Relationship Quality in Brown Capuchin Monkeys

5.1. Introduction

Social relationships vary in content (e.g. sexual, parenting, affiliation or conflict), quality (e.g. the intensity of affiliation or aggression), and patterning (e.g. frequency and temporal stability) (Hinde 1976). Frequent affiliative interactions and low rates of agonism can result in higher-quality relationships, which in turn can affect an individual's behaviour and fitness in a variety of ways. For example, individuals with higher-quality relationships may show reduced behavioural and/or physiological responses to stress (Castles et al. 1999; Heinrichs and Domes 2008; Majolo et al. 2009). Individuals with higher-quality relationships may also have greater opportunities for mating (Schulke et al. 2010; Massen et al. 2012; Langergraber et al. 2013), higher rates of agonistic support (Koyama et al. 2006; Schino 2007; Fraser and Bugnyar 2010), priority access to food (Janson 1990), better protection from infanticide (van Schaik and Kappeler, 1997; Ebensperger 1998; Palombit 2000; Borries et al. 2010), and/or experience lower levels of conflict (Fraser and Bugnyar 2010; Rebeccini et al. 2011; Tiddi et al. 2011). For juveniles, the formation of social relationships can be particularly important in terms of integrating themselves within their group (Hinde and Spencer-Booth 1967). Finally, individuals with higher-quality relationships can have greater longevity and increased offspring survivorship (Silk et al. 2003, 2010). Relationships are thus an important adaptive strategy in animals. Understanding the nature and source of variability in animals' social relationships can therefore lead to a better understanding of how animals make social decisions, particularly in terms of cooperation and conflict with others, and how those decisions shape individual and reproductive fitness.

5.1.1. Factors Affecting Social Relationships

Variation in the content and quality of social relationships between pairs of animals is often explained through a set of basic social rules. Energetic constraints on each sex, for example, are one such factor. Males and females differ in their reproductive physiology and extent of investment in offspring; thus, social decision-making in each sex is likely to be motivated by different factors (Trivers 1972). For instance, females develop strong and discriminatory bonds with other related females, which may serve to regulate agonistic encounters resulting from increase feeding competition (van Schaik 1989; Boinski et al. 2002). Females also form coalitions with each other as a defence against food competitors and aggressive males (Smuts and Smuts 1993). Lastly, females compete with one another to establish and maintain relationships with high-quality males (i.e. those with “good genes”, and those that provide greater protection and access to food; van Schaik 1983; Bro-Jorgensen 2002). As such, females often establish relationships with high-ranking males (Clutton-Brock and Huchard 2013). Males, on the other hand, compete with one another to gain access to sexually receptive females (McDonald 1989; Koyama et al. 2012; Clutton-Brock and Huchard 2013). In some species, this may lead to conflict (e.g. physical fights), while in other species this may lead to more cooperative strategies to reduce mating competition (e.g. tolerance or active bonding; Packer and Pusey 1982; Diaz-Munoz et al. 2014).

Position within a dominance hierarchy, or “social rank”, is another factor shaping the social relationships of animals. Relative ranks can be established via the outcome of aggressive interactions or approach-retreat between group members (Hinde and Datta 1981; Issa et al. 1999). Generally, higher-ranking individuals have greater control over the behaviour of others within their group. For this reason, most animals compete for higher dominance within their group since this may result in fitness-related benefits (e.g. von Holst et al. 2002; Schulke et al. 2010; Clutton-Brock and Huchard 2013). Dominance rank is generally associated with preferential access to resources (e.g. food or mating partners) and greater reproductive success (Janson 1990; von Holst et al. 2002; Schulke et al. 2010; Clutton-Brock and Huchard, 2013). Social network analyses have revealed that dominant individuals occupy central positions within their groups, and appear to play an important role in maintaining group stability (e.g. Flack et al. 2006). Beyond aggression, however, social rank also facilitates the nature and occurrence of different forms of cooperative behaviour among group members which, in turn, may lead to social manoeuvring of one’s status within a hierarchy. For example, subordinates exchange social services like grooming and food sharing to gain tolerance and support from higher-ranking individuals (Schino, 2007; Tiddi et al. 2011). Individuals may also form alliances with each other to win contests they would otherwise lose (e.g. access to food or mates; Packer and Pusey 1982; Harcourt 1988). Lastly, alpha males may depend on allies to maintain their status position and will therefore grant tolerance and direct affiliative behaviour towards those individuals that give him coalitionary support (e.g. Duffy et al. 2007).

In terms of developmental trajectories, animals experience changes in behaviour, morphology and physiology, which in turn can influence how they interact with others. Social rank among males tends to increase with age and length of residency in the group (Clutton-Brock and Huchard 2013), which may be due to age-associated changes in testosterone, a hormone linked to aggressive behaviour (Lincoln and Ratnasooriya 1996). Prior experience, and thus memory, of past social encounters between group members also likely affects animals' future social decision-making (Fernald 1976; Silk 2002). Relationship quality is typically higher among group members that have known each other for a longer period (e.g. the philopatric sex), since familiarity may facilitate the predictability of each other's behaviour (Koski et al. 2012; Kurvers et al. 2013). In species such as chimpanzees, individuals become increasingly intolerant of others as they age (Wobber et al. 2010), which in turn may place constraints on the breadth and quality of their social relationships with others in their group. Collectively, age-associated variables play an important role in how social relationship quality varies over time.

Nepotistic biases towards related group members (or kin selection) are often used to explain the cooperative behaviour of animals in groups (i.e. actions that increase the fitness of the receiver at the expense of the giver; Clutton-Brock 2002). For example, in many species, there are often clear nepotistic biases towards kin in terms of how individuals allocate affiliative acts to others, such as grooming, support, tolerance, and food sharing (Koyama 2003; Silk et al. 2004; Perry et al. 2008; Hirsch et al. 2012; Silk et al. 2013; Smith 2014). In female-bonded species (sensu Wrangham 1980), dominance hierarchies are largely based on matrilineal inheritance, whereby offspring will usually inherit a position within the group's social rank just below their mother (Lee and Oliver 1979; Kutsukake 2000; Engh et al. 2000). Thus, collectively, kinship influences the nature and quality of animals' social relationships, which in turn may facilitate their level of social success within a group.

While many researchers have focused on how sex, rank, age, and kinship influence animals' social relationships, such variables do not always explain the range of variation reported across studies. Hirsch et al. (2012) found that kinship shaped affiliative, but not agonistic, interactions among ring-tailed coatis (*Nasua nasua*). In barnacle geese (*Branta leucopsis*), Kurvers et al. (2013) found that social rank does not affect social affiliation, whereas kinship does. In brown capuchin monkeys, Tiddi et al. (2011) found that social tolerance was unrelated to kinship and rank, but weakly related to sex. Thus, it is clear that not all basic social rules contribute equally to the content and quality of animals' social relationships; rather, marked variation can exist both within and between studies in terms of which basic social rules are important explanatory variables.

The potential role of personality "homophily" in animal social relationships, i.e. affinity towards individuals with similar personalities (Massen and Koski 2014), has recently been recognized. Among humans, individuals that score similarly on Extraversion, Agreeableness, and Openness have a tendency to form stronger social relationships with each other than those individuals more dissimilar in those traits (Selfhout et al. 2010; Nelson et al. 2011). In rhesus macaques, individuals preferentially affiliate with group members that are more similar in terms of Equability (e.g. calm/slow) and Adaptability (e.g. flexible/gentle; Weinstein and Capitanio 2008). Such studies suggest that personality homophily may promote familiarity and predictability in partners' behaviour once a relationship has been established, and may also be an adaptive strategy that promotes genetic compatibility between potential mates. Indeed, in humans, perceived similarity in personality promotes friendship intensity and trust (Bauer and Green 1996; Selfhout et al. 2009). In studies of zebra finches (*Taeniopygia guttata*), similarity in parental personality traits (exploration and aggression) and the combination of personalities within breeding pairs is a positive indicator of future offspring quality (e.g. body mass; Schuett et al. 2011). However, while personality homophily explains variance in social relationships, the extent to which such similarities are independent of any effects from basic social rules remains poorly understood. For example, similarities in social rank may underlie similarities in bold or aggressive personality traits - which are often associated with social rank in many species (Chapter 3). Additionally, given that personality traits can be heritable (Jang et al. 1996; van Oers et al. 2004), personality homophily between related social partners may simply reflect animals' nepotism towards kin.

Weinstein and Capitanio (2008) found that personality homophily explains variation in the strength of social relationships formed between rhesus macaques even after controlling for kinship, sex, and rank, indicating that personality homophily was an important factor shaping the social relationships of these animals beyond basic social rules. More data are needed on other species to investigate the role that personality homophily plays in animal social relationships, and how similarities in particular personality traits co-associate with intra-group variation in social relationships.

The present study investigates the relative roles of basic social rules and personality homophily in the social relationship quality of two captive groups of brown capuchin monkeys housed at the 'Living Links to Human Evolution' Research Centre, Edinburgh Zoo, UK (MacDonald and Whiten 2011). Capuchins are an interesting model with which to test hypotheses regarding personality homophily given their variable and complex social relationships both within and between groups (Fragaszy et al. 2004), their relatively tolerant nature towards others (including non-kin and particularly infants) (Fragaszy et al. 2004), and their generally low rates of agonism (Cooper et al. 2001). In particular, unlike the social structures of many Old World primates (e.g. vervet monkeys, baboons, rhesus macaques), which appear to be strongly influenced by basic social rules (e.g. Chapais 1992), studies on captive and wild capuchins often report mixed results in terms of the extent to which different basic social rules explain variation in capuchins' social relationships. Schino et al. (2009) and Tiddi et al.

(2012) found that capuchins preferentially give coalitionary support to their kin, whereas Ferreira et al. (2006) found no such effects within their study population. While some studies have reported that capuchins groom "down" the hierarchy (Parr et al. 1997), others have found no significant relationship between grooming and rank (Schino et al. 2009), or have reported that their study animals groom "up" the hierarchy (Tiddi et al. 2012). Lastly, while several studies have shown that capuchins typically engage in affiliative acts with others that are similar in rank (Parr et al. 1997; Tiddi et al. 2012), others have found no such effects among their subjects (Schino et al. 2009). Thus, individual differences in personality may be one possible factor contributing to variation in capuchins'' social relationships beyond basic social rules.

In Chapter 4, a principal components analysis of ten social behaviours suggested that the Living Links capuchins have two dimensions to their social relationships: 1) an affiliative component, which was characterized by high loadings for behaviours like grooming, social foraging, and coalitions, and 2) an agonistic component, which was characterized by high loadings by aggression and displacements from monopolizeable food resources. In this chapter, dyadic scores on each relationship component are correlated with differences in each social partner's relative degree of relatedness ("kinship"), sex, age, and social rank. Component scores are then correlated with differences in each partner's relative scores on five personality traits (Assertiveness [e.g. *bullying*, *aggressive*], Openness [e.g. *playful*, *curious*], Sociability [e.g. *friendly*, *affectionate*], Neuroticism [e.g. *erratic*, *unpredictable*], and Attentiveness [e.g. *helpful*, *decisive*] (see Chapter 3). In light of previous work on personality homophily, it was hypothesized that capuchins with similar personalities would share higher-quality relationships (i.e. higher affiliative scores, lower agonistic scores) with each other than group members with more dissimilar personalities (Hypothesis 1). Additionally, it was hypothesized that after controlling for basic social rules, personality homophily would still be a significant predictor of dyadic differences in subjects' affiliative and agonistic relationship qualities (Hypothesis 2).

5.2. Methods and Materials

5.2.1. Measuring Social Relationship Quality

Measures of social relationship quality were calculated per non-infant group member, resulting in a total of 73 dyads. Ten behavioural measures (Tables 15-16 in Chapter 4) were calculated per dyad and subjected to a principal components analysis (PCA) with varimax rotation. A scree test and parallel analysis recommended two components to extract from the PCA (see details in Chapter 4). Components with high loadings (i.e. |0.7|) and/or those with four or more loadings greater than |0.4| were considered robust (Guadagnoli and Velicer 1988; Field 2009). For each component, z-scores were calculated per dyad (Field 2009). The first component was characterized by moderate to high loadings from affiliative behaviours (e.g. food sharing, coalitions, and grooming), while the second component was characterized by high loadings from agonistic behaviours (i.e. rates of aggression and aggression symmetry). The higher a monkey dyad scored on a given component, the more affiliative/agonistic the relationship. A higher score on the affiliative component and lower score on the agonistic component was indicative of an overall "higher-quality" relationship for a given dyad.

5.2.2. Basic Social Rules

Social rank was determined by calculating David's Scores (DS) using data on the win/loss outcomes of each monkey's agonistic interactions. Details of these calculations are provided in Chapter 2. Similarity in rank was calculated for each dyad by subtracting one partner's DS from the other partner's score, and taking the absolute value (hereafter "rank distance").

Age and sex were known for each study subject (Chapter 2). Age similarity was calculated for each dyad by subtracting one partner's age (in years) from the other partner's age, and taking the absolute value (hereafter "age distance"). To examine the effect of sex on relationship quality, dyads were classified according to whether partners were male-male, male-female, or female-female. In total, there were 25 male-male dyads, 39 male-female dyads, and 9 female-female dyads. Coefficients of relatedness (r) (hereafter "kinship") were estimated between each monkey using the monkeys' pedigrees (further details in Chapter 2). Coefficients of relatedness were used as a measure of kinship similarity between partners within a dyad (hereafter "kinship distance").

5.2.3. Personality Homophily

Data and analyses on subjects' personalities are provided in Chapter 3. Five distinct personality traits were reliably demonstrated and behaviourally validated in a large sample (N=127 subjects from 7 sites) of brown capuchin monkeys: Assertiveness (e.g. *aggressive*, *bullying*), Openness (e.g. *curious*, *active*), Attentiveness (e.g. *organized*, *perceptive*), Neuroticism (e.g. *excitable*, *erratic*), and Sociability (e.g. *affectionate*, *friendly*). Subjects' scores per trait were calculated and used in this study. For each dyad, personality homophily was calculated for each personality trait by subtracting one partner's score from the other partner's score, and taking the absolute value (hereafter "personality distance").

5.2.4. Statistical Analyses

Pearson correlations were used to examine bivariate associations between relationship scores and similarity in age, kinship, rank, and the five personality traits. Three separate univariate regressions (one for each relationship score) were used to test for the effects of sex similarity. Finally, three multiple regressions (one for each relationship score) were used to test whether the effect of personality similarity contributed to relationship scores over and above the contribution of basic social rules.

Because the same 18 subjects were represented in all 73 dyads, observations were not independent. Therefore bias-corrected and accelerated bootstrapping procedures were used to generate 95% confidence intervals (Efron 1987; Davison and Hinkley 1997). Sampling was conducted with replacement (5000 replicates). Bootstrapping was conducted using the 'boot' function in R (Canty and Ripley 2014).

5.3. Results

5.3.1. Basic Social Rules

Dyads similar in age and rank shared significantly lower agonistic scores (Table 22; Figure 22 and 23). In terms of overall relationship quality (i.e., the difference between partners' affiliative and agonistic scores), monkeys similar in rank shared higher-quality relationships than did other dyads. Kinship and sex were not significantly related to affiliative/agonistic scores or overall relationship quality.

Table 22. Pearson correlations between similarities in age, kinship, rank, and personality traits and affiliative/agonistic scores and relationship quality (i.e. difference between affiliative and agonistic scores).

	Affiliative Scores		Agonistic Scores		Overall Quality	
	r	95% CI	r	95% CI	r	95% CI
Age	0.05	[-0.12, 0.31]	**0.19**	**[0.03, 0.49]**	-0.10	[-0.29, 0.12]
Kinship	0.06	[-0.21, 0.29]	-0.17	[-0.37, 0.05]	0.16	[-0.08, 0.36]
Rank	-0.14	[-0.29, 0.04]	**0.47**	**[0.23, 0.66]**	**-0.44**	**[-0.61, -0.24]**
Assertiveness	0.04	[-0.19, 0.25]	0.03	[-0.13, 0.20]	0.01	[-0.19, 0.19]
Openness	**-0.22**	**[-0.37, -0.00]**	**0.42**	**[0.23, 0.57]**	**-0.45**	**[-0.58, -0.28]**
Neuroticism	-0.13	[-0.32, 0.13]	0.13	[-0.09, 0.29]	-0.19	[-0.35, 0.03]
Sociability	**-0.33**	**[-0.46, -0.17]**	0.04	[-0.16, 0.24]	**-0.26**	**[-0.41, -0.08]**
Attentiveness	-0.05	[-0.26, 0.19]	0.09	[-0.10, 0.25]	-0.10	[-0.27, 0.08]

Note. 95% CI = bootstrapped 95% confidence intervals. *df* = 63. "Overall Quality" = difference between affiliative and agonistic component scores per dyad. Negative correlation coefficients indicate that partners that are similar in personality score higher on a given relationship measure.

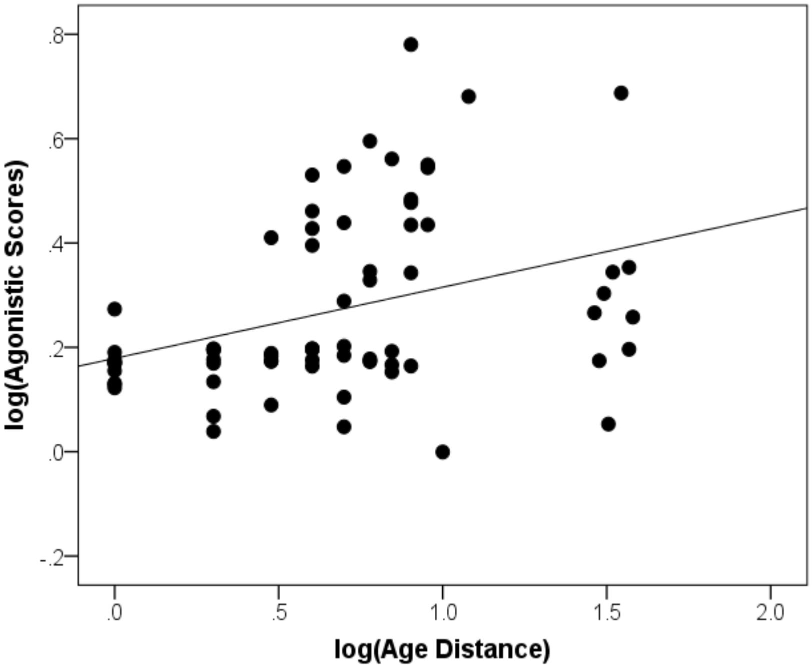


Figure 22. Relationship between age distance and agonistic relationship scores.

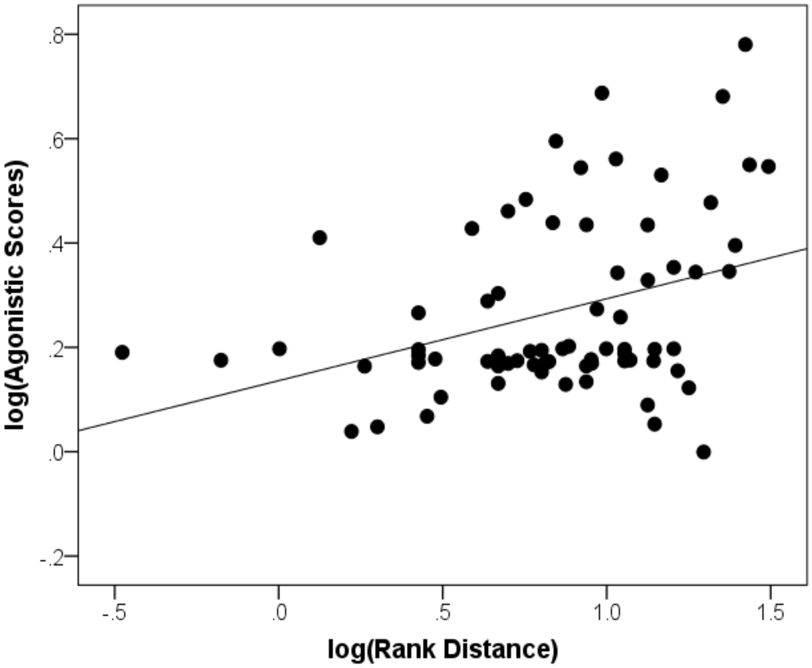


Figure 23. Relationship between rank distance and agonistic scores.

5.3.2. Personality Homophily

Dyads similar in Openness and Sociability shared higher affiliative scores (Table 22; Figure 24 and 25). Dyads similar in Openness shared significantly lower agonistic scores. In terms of overall relationship quality, monkeys similar in Openness and Sociability shared higher-quality relationships than did other dyads. The other three personality traits were not significantly related to affiliative/agonistic scores or overall relationship quality.

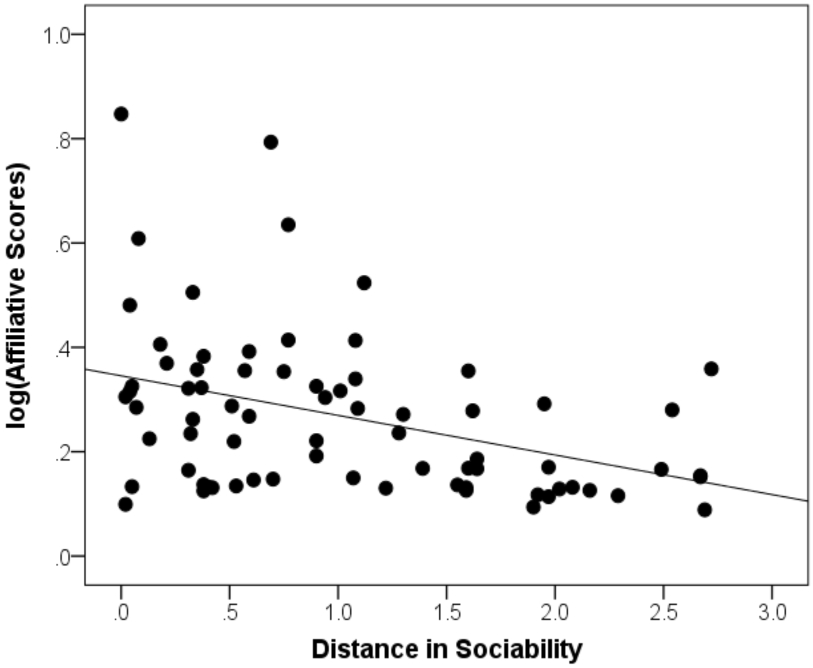


Figure 24. Relationship between dyadic differences in Sociability and affiliative relationship scores.

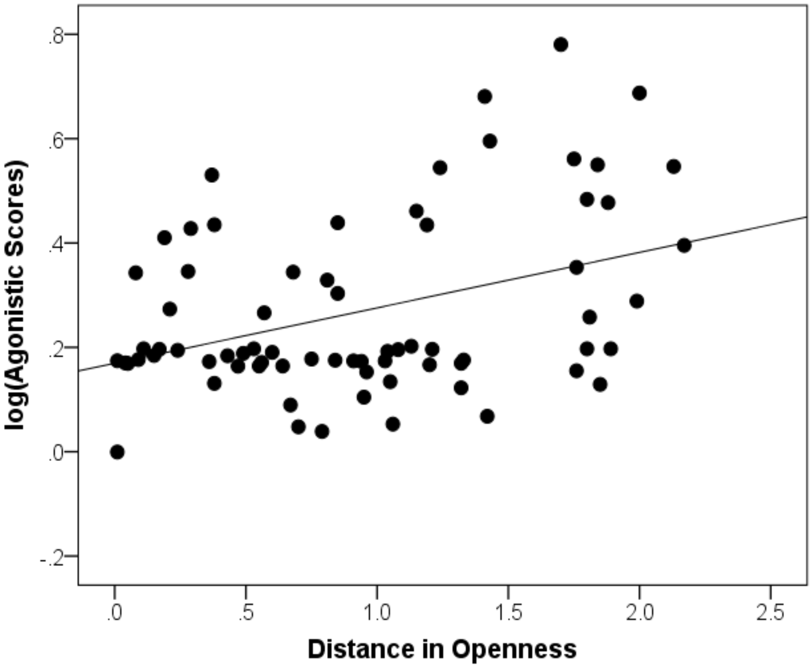


Figure 25. Relationship between dyadic differences in Openness and agonistic relationship scores.

The results of the multiple regression analysis are presented in Table 23. The sole independent predictor of affiliative scores was Sociability; monkeys that differed more in Sociability were less affiliative. The sole independent predictors of agonistic scores were rank and Openness; monkeys that differed more in rank or Openness were more agonistic. The sole independent predictors of total relationship quality were rank, Openness, and Sociability; higher relationship quality was associated with dyads who were more similar in rank, Openness, and Sociability.

Table 23. Independent effects of basic social rules and personality variables on affiliative scores, agonistic scores, and relationship quality (i.e. difference between affiliative and agonistic scores).

	Affiliative Scores				
Effect	β	SE	t	P	95% CI
Intercept	-0.05	0.25	-0.22	0.83	[-0.55, 0.72]
Sex	0.27	0.23	1.19	0.24	[-0.13, 0.81]
Age	0.00	0.01	0.18	0.85	[-0.03, 0.03]
Rank	-0.10	0.13	-0.79	0.43	[-0.44, 0.06]
Kinship	-0.40	0.59	-0.68	0.50	[-2.01, 0.70]
Assertiveness	0.04	0.14	0.27	0.78	[-0.20, 0.38]
Openness	-0.15	0.14	-1.09	0.28	[-0.45, 0.05]
Neuroticism	-0.10	0.13	-0.76	0.45	[-0.38, 0.17]
Sociability	**-0.31**	**0.13**	**-2.41**	**0.019**	**[-0.62, -0.11]**
Attentiveness	0.04	0.13	0.26	0.79	[-0.25, 0.25]
	Agonistic Scores				
Effect	β	SE	t	P	95% CI
Intercept	-0.09	0.23	-0.39	0.69	[-0.63, 0.35]
Sex	-0.02	0.21	-0.08	0.94	[-0.41, 0.41]
Age	0.01	0.01	0.91	0.37	[-0.01, 0.05]
Rank	**0.39**	**0.12**	**3.19**	**0.002**	**[0.12, 0.73]**
Kinship	0.03	0.54	0.06	0.95	[-0.99, 1.28]
Assertiveness	-0.10	0.13	-0.81	0.42	[-0.36, 0.10]

Openness	**0.26**	**0.13**	**2.04**	**0.046**	**[0.01, 0.57]**
Neuroticism	0.04	0.12	0.35	0.72	[-0.18, 0.32]
Sociability	-0.01	0.12	-0.13	0.90	[-0.24, 0.18]
Attentiveness	-0.01	0.12	-0.06	0.95	[-0.22, 0.19]
			Total Quality		
Effect	β	SE	t	P	95% CI
Intercept	0.02	0.22	0.11	0.91	[-0.44, 0.49]
Sex	0.21	0.20	1.01	0.32	[-0.13, 0.72]
Age	-0.01	0.01	-0.51	0.61	[-0.04, 0.02]
Rank	**-0.35**	**0.12**	**-2.96**	**0.004**	**[-0.64, -0.12]**
Kinship	-0.31	0.52	-0.59	0.56	[-1.39, 0.76]
Assertiveness	0.10	0.12	0.82	0.42	[-0.09, 0.41]
Openness	**-0.30**	**0.13**	**-2.36**	**0.021**	**[-0.53, -0.08]**
Neuroticism	-0.10	0.12	-0.87	0.39	[-0.32, 0.07]
Sociability	**-0.21**	**0.11**	**-1.84**	**0.070**	**[-0.49, -0.04]**
Attentiveness	0.03	0.12	0.26	0.80	[-0.15, 0.24]

Note. Significant results ($P < 0.05$) highlighted in bold; *df* in all cases = 63. Negative parameter coefficients (β) indicate that partners that are similar in personality or a basic social rule also have higher scores on that particular relationship measure.

5.4. Discussion

In light of previous work on personality homophily in animals, it was hypothesized that capuchins with similar personalities would share higher-quality relationships (i.e. higher affiliative scores, lower agonistic scores) with each other than group members with more dissimilar personalities (Hypothesis 1). Additionally, it was hypothesized that after controlling for basic social rules, personality homophily would still be a significant predictor of dyadic differences in the quality of subjects’ affiliative and agonistic relationships (Hypothesis 2). Supporting both hypotheses, lower distance in Sociability between social partners positively predicted dyadic differences in affiliative relationship scores, while distance in Openness negatively predicted dyadic differences in agonistic relationship scores; in other words, partners that were more similar in Sociability and Openness shared significantly higher-quality social relationships than other dyads. Controlling for kinship, age, sex, and rank, homophily in both personality traits had an independent effect on dyadic variability in the social relationships of these capuchins.

A study of chimpanzees reported that similarity in sociable personality between partners positively correlated with the amount of time social partners spent in close proximity to each other; that is, the amount of time subjects were “affiliated” (Massen and Koski 2014). In humans, studies have shown that similarities in Openness play an important role in maintaining friendships (Costa and McCrae 1992). In the present study, similarity in Sociability (presumably analogous to the sociability trait measured in chimpanzees) and Openness (which is analogous to human Openness; Morton et al. 2013) were correlated with subjects’ affiliative and agonistic relationship scores, respectively. Such overlap in results from phylogenetically distant species (Steiper and Young 2006) suggests that the association between affiliative relationship quality and homophily for particular personality traits has a long evolutionary history.

Distance in Openness was negatively related to agonistic relationship scores, indicating that monkeys who were more similar in Openness had fewer conflicts compared to other dyads.

In Chapter 3, individual differences in Openness were found to be negatively related to differences in the amount of time subjects were aggressive in total. Therefore, monkeys that were more similar in terms of this personality trait may have been more compatible due to their lower levels of hostility.

As in capuchins, personality homophily among rhesus macaques contributes to the quality of subjects' social relationships beyond what can be explained merely by basic social rules (Weinstein and Capitanio 2008). However, in rhesus macaques, basic social rules still had independent effects on the quality of partners' affiliative relationships, whereas in capuchins, personality homophily was the only significant predictor of affiliative relationship quality. One possible explanation could be that in the present study, a single measure of affiliative relationship quality was derived from a principal components analysis containing eight affiliative behaviours (Chapter 4), whereas in the macaque study, hypotheses regarding personality homophily were tested on individual behaviours (e.g. play and proximity; Weinstein and Capitanio 2008). Therefore, while other personality traits may have differential effects on capuchins' affiliative relationships in terms of individual behaviours, the present study highlights the importance of personality homophily in terms of capuchins' *cumulative* affiliative relationship quality (i.e. combined behavioural measures).

Basic social rules also predicted social relationship quality among the LL capuchins. In particular, distance in age and social rank were both positively related to agonistic relationship scores; meaning, individuals that were more similar in age and rank had less tempestuous relationships with one another. These findings are suggestive of the typical behaviour of capuchins: older and higher-ranking monkeys generally direct aggression towards younger and lower-ranking group members (Janson 1990).

One important area of future research is understanding causality between personality homophily and social relationship quality; that is, whether individuals seek social affiliation with others that are more similar in personality, or whether affiliated individuals somehow develop these similarities over time. In humans, for example, perceived similarity in personality traits facilitates friendship intensity but also enhances how partners perceive similarities in their personality (Selfhout et al. 2009; Linden-Andersen et al. 2009). Longitudinal data are therefore needed to examine this issue further.

5.5. Conclusions

Across a variety of taxa, personality homophily appears to play an important role in shaping relationship quality among social partners. In the present study, it was found that similarities in personality were related to both the affiliative and agonistic components of capuchins' social relationships, and more importantly, these effects were independent of any effects from basic social rules. Similarity in personality should therefore raise intriguing questions regarding the mechanisms behind relationship formation and maintenance as it may facilitate partner compatibility.

CHAPTER 6

Social Networks in Brown Capuchin Monkeys

Photograph 6

CHAPTER 6

Social Networks in Brown Capuchin Monkeys

6.1. Introduction

"Social structure", or the accumulation of interactions that take place between individuals within a population over time (Hinde 1976), is one of the most important aspects of animal behaviour. Social structure is related to migration patterns, present and future decision-making, population growth rates, gene flow, and information and disease transmission (Morin et al. 1994; Loehle 1995; Whitehead 2008; Hoppitt et al. 2010; Mysterud et al. 2011). At the individual level, social structure is an important predictor of animals' exposure to predators, access to resources (e.g. food and mates), and support from others (Janson 1990; Kie 1999; Silk et al. 2004; Loretto et al. 2012). Social structure can therefore impact the fitness of animals (e.g. Jones and Riechert 2008; Selonen et al. 2013).

Personality corresponds to individual differences in animals' general behavioural decision-making across time and contexts, such as social interactions with others (Pike et al. 2008; Seyfarth et al. 2014; Chapter 3), risk-taking (Zuckerman and Kuhlman 2000; van Oers et al. 2004), coping strategies (Connor-Smith and Flachsbart 2007), and motivation (Sears 1944; Dweck and Leggett 1988; Corr et al. 2013). Personality is therefore potentially a good predictor of variability in social structure. For example, Pike et al. (2008) found that bolder sticklebacks (*Gasterosteus aculeatus*) had many social connections that were evenly spread throughout a shoal, whereas shyer fish had stronger affiliations with fewer individuals. Aplin et al. (2013) found that in birds, more proactive (fast-exploring) individuals maintained weak social relationships with a large number of conspecifics, while more reactive (slow-exploring) birds formed more stable relationships. Lastly, Godfrey et al. (2012) found that in male sleepy lizards (*Tiliqua rugosa*), less aggressive individuals were more strongly connected to females in their social network, compared to more aggressive males. To date, however, the role that personality plays in the social structure of animals remains poorly understood. While some studies report that boldness and patterns of sociality among animals are closely associated (e.g. Pike et al. 2008; Dahlbom et al. 2011), Kurvers et al. (2013) found no effect of boldness on the foraging associations and mate choice patterns of barnacle geese. Further studies are therefore needed to understand why personality might relate to social structure in some cases, but not in others. Previous work examining associations between personality and social structure have also largely focused on just one or two personality traits within the same study population (e.g. boldness and proactivity; Pike et al. 2008; Dahlbom et al. 2011; Aplin et al. 2013). As such, further data are needed on a broader range of personality traits to test whether some traits are more important than others in terms of how animals organize themselves within groups. Finally, only a few studies have examined the extent to which personality traits contribute to social structure *beyond* basic social rules. In studies of fish, for example, individual differences in boldness reflect differences in social networking strategies (e.g. Pike et al. 2008), but may also reflect differences in dominance rank (e.g. Dahlbom et al. 2011). In humans, Neuroticism is associated with larger social networks (i.e. the number of social partners an individual affiliates with; Whitehead 2008), but is also related to greater familial support (McHugh and Lawlor 2012). Thus, in humans, the association between Neuroticism and social networks may be mediated through both variables' relationship with kinship. Weinstein and Capitanio (2008) found that after controlling for the effects of basic social rules, personality was still related to patterns of social interaction among adolescent rhesus macaques. Therefore, further data are needed on other species to determine the extent to which personality contributes to structural variation within animal societies independently from basic social rules.

This chapter investigates relationships between personality and social structure in brown capuchin monkeys. Capuchins are an interesting model with which to test hypotheses regarding associations between personality and social structure associations given that they exhibit multiple dimensions to their personality (Chapter 3), their social structure is variable and complex both within and between groups (Fragaszy et al. 2004), they are relatively tolerant towards others (including non-kin and particularly infants) (Fragaszy et al. 2004), and compared to many primates they generally exhibit low rates of agonism (Cooper et al. 2001). Unlike many Old World primates (e.g. vervet monkeys, baboons, rhesus macaques), which appear to be strongly influenced by basic social rules when making social decisions (e.g. Chapais 1992), studies on captive and wild capuchins have so far reported mixed results in terms of how basic social rules explain variation in capuchins’ social structure. For example, Schino et al. (2009) and Tiddi et al. (2012) found that capuchins preferentially give coalitionary support to their kin, whereas Ferreira et al. (2006) found no such effects within their study population. Additionally, while some studies have reported that capuchins groom “down” the hierarchy (Parr et al. 1997), others have found no significant relationship between grooming and rank (Schino et al. 2009), or have reported that their study animals groom “up” the hierarchy (Tiddi et al. 2012). Finally, while several studies have shown that capuchins typically engage in affiliative acts with others that are similar in rank (Parr et al. 1997; Tiddi et al. 2012), others have found no such effects among their subjects (Schino et al. 2009). In Chapter 5, it was found that dyadic similarities in personality among capuchins were significant predictors of the quality of their social relationships, even after controlling for possible effects from basic social rules. Thus, considering that social relationships are the building blocks of social structure (Hinde 1976), it is likely that individual differences in personality are an additional factor contributing to variability in the social structure of capuchins.

In Chapter 3, five personality traits were identified and behaviourally-validated in brown capuchin monkeys: Assertiveness (e.g. *aggressive* and *bullying*), Openness (e.g. *curious* and *playful*), Neuroticism (e.g. *erratic* and *unpredictable*), Sociability (e.g. *friendly* and *affectionate*), and Attentiveness (e.g. *decisive* and *predictable*). In light of recent advances in the use of social network analysis (SNA) in studies of animal social structure (discussed in Chapter 2), the present study investigated how each of these five personality traits contributed to the social network structure of two captive groups of brown capuchin monkeys housed at the "Living Links to Human Evolution" Research Centre, UK. It was hypothesized that individual differences in the personality of these capuchins would be significantly related to differences in their social network position (Hypothesis 1), and that these associations would be independent of any effects from basic social rules (Hypothesis 2).

6.2. Methods and Materials

6.2.1. Behavioural Sampling

Fifty-four hours of focal observations were recorded between May and August, 2011, totalling 3 hours per individual. Monkeys were sampled evenly between 9:00 and 17:30. Using point sampling methods (Martin and Bateson 2007), group members within two body lengths from the focal were recorded at 1-min intervals for ten minutes. Further details of data collection can be found in Chapter 2.These behavioural data were used to construct social networks.

6.2.2. Social Network Analysis

Individual differences in social network position are represented in terms of each monkey's eigenvector centrality (hereafter "centrality"). Centrality measures how well each individual is associated with other individuals and how well its close associates are themselves associated (Croft et al. 2008).

6.2.3. Network Validation

In wild and captive capuchins, individuals who spend more time in close proximity are less likely to engage in conflict and more likely to engage in affiliative behaviour (Chapter 2); the affiliative and agonistic relationship quality scores that were calculated in Chapter 4 are used here to validate this notion within the Living Links capuchins. For each component, z-scores were calculated per social dyad, and from these, it was possible to calculate the mean quality of relationships each monkey had with others (Table 18 in Appendix). A higher average score on the affiliative component and a lower average score on the agonistic component indicated that a given monkey had "higher-quality" relationships within their group compared to other monkeys. For the purpose of this study, subjects' average scores on the agonistic component were subtracted from their average scores on the affiliative component, thereby yielding an overall "relationship quality score" for each monkey.

Scores on spatial proximity centrality were positively correlated with monkeys' mean relationship quality with others in their group (r=0.502, P=0.034, N=18; Figure 27). Thus, in this population of monkeys, scores on spatial network centrality were considered to be reflective of both subjects' affiliative and agonistic relationships with each other (i.e. "social embeddedness").

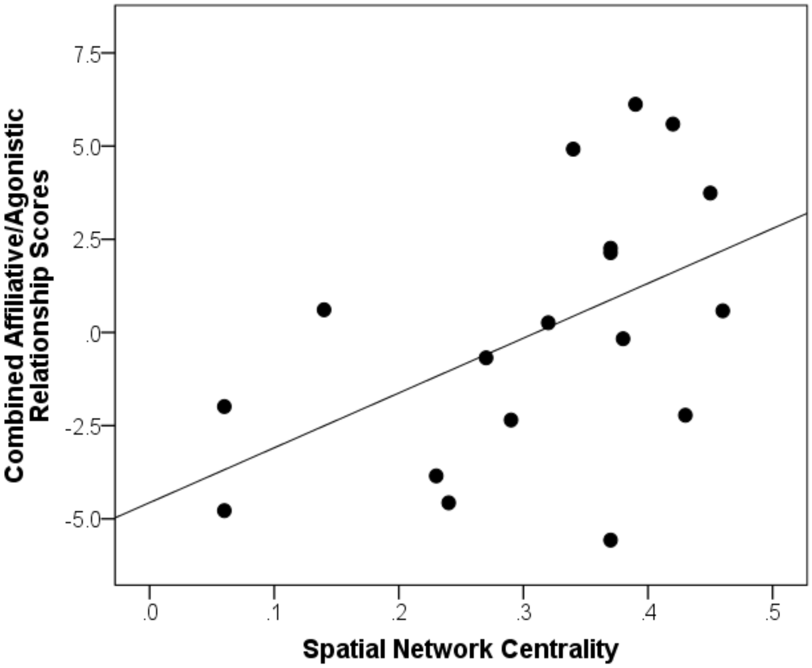


Figure 26. Relationship between individual differences in spatial network centrality and monkeys' mean relationship quality with others in their group (i.e. "social embeddedness").

6.2.4. Testing Network Robustness

The robustness of each group's social network was tested by randomly removing 50% of observations, re-calculating monkeys' centrality, and correlating these scores with those calculated using 100% of the data. The scores were highly correlated (r=0.987, P<0.001, N=18), indicating that the data were robust.

6.2.5. Basic Social Rules

Age (in years) and sex were known for each study subject (Chapter 2). Social rank was determined by calculating David's Scores (DS) using data on the win/loss outcomes of each monkey's agonistic interactions. Details on these calculations are provided in Chapter 2. Each monkeys’ average coefficient of relatedness (r) (hereafter “kinship”) with others in their group was estimated through pedigrees (further details in Chapter 2).

6.2.6. Personality

Data and analyses on subjects’ personalities are provided in Chapter 3 and Table 19 in the Appendix. Five distinct personality traits were reliably demonstrated and behaviourally validated in a large sample (N=127 subjects from 7 sites) of brown capuchin monkeys: Assertiveness (e.g. *aggressive*, *bullying*), Openness (e.g. *curious*, *active*), Attentiveness (e.g. *organized*, *perceptive*), Neuroticism (e.g. *excitable*, *erratic*), and Sociability (e.g. *affectionate*, *friendly*). Subjects’ scores per trait were calculated and used in this chapter.

6.2.7. Statistical Analyses

Pearson correlations were used to examine relationships between variables. Partial correlations were used to control for specific variables. Bootstrapped t-tests (replacement=1,000) were used to examine differences in the network centrality of each sex. Residual scores from regression analyses between monkeys’ network centrality scores and their respective age, rank, and personality were used when testing for independent effects of sex on network centrality (Field 2009). All basic social rules and personality traits were entered stepwise into a multiple regression model to test for their relative contribution to variation in monkeys’ social network centrality (Field 2009). Bootstrapped t-tests were conducted in R (version 3.0.1), while all other analyses were conducted in IBM SPSS Statistics 19. Social networks were constructed in SOCPROG 2.4; associations were defined using a simple ratio index (Whitehead 2009).

6.3. Results

6.3.1. Social Networks and Basic Social Rules

The sociograms for East and West groups are provided in Figures 28 and 29, respectively. Centrality scores were positively related to social rank (r=0.625, P=0.006, N=18; Figure 30), while kinship and age were not significantly associated with centrality (kinship: r=0.0, P=1.0, N=18; age: r=0.214, P=0.394, N=18). There were no significant differences in the centrality of males versus females (t=-1.173, P=0.258, df=16; Bootstrap=P=0.999). Controlling for kinship age, and sex, social rank was still positively related to centrality (r=0.624, P=0.013, df=13).

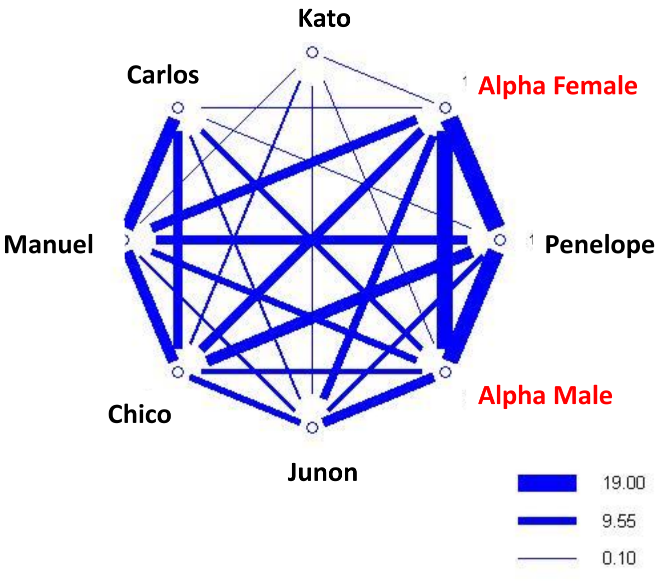


Figure 27. Sociogram for East group.

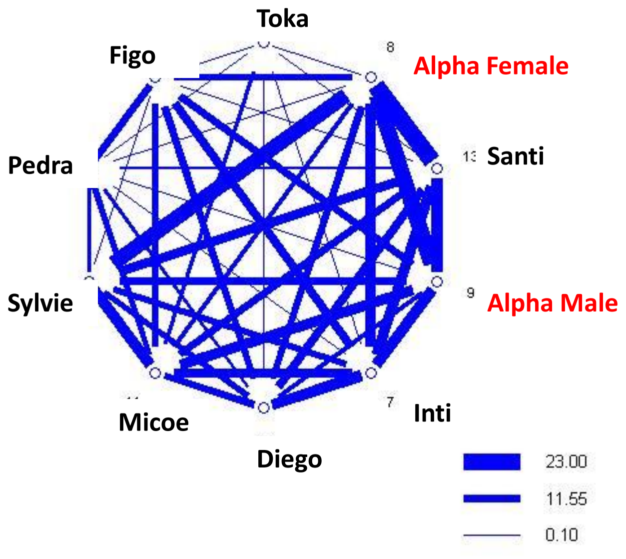


Figure 28. Sociogram for West group.

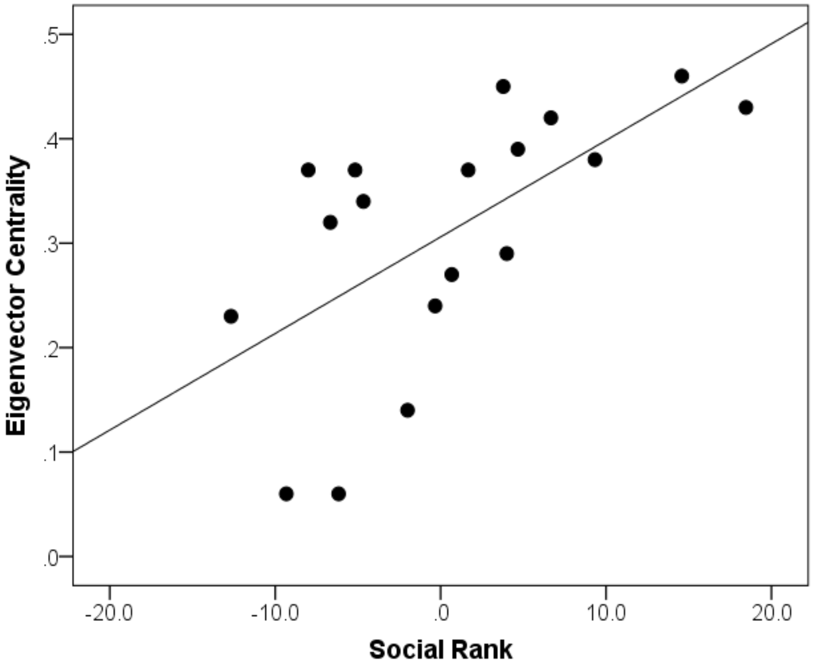


Figure 29. Relationship between social network centrality and social rank (based on David's scores); positive David's scores indicate higher social rank.

6.3.2. Social Networks and Personality

Centrality was positively correlated with Assertiveness (r=0.543, P=0.02, N=18; Figure 31), and negatively correlated with Neuroticism (r=-0.482, P=0.043, N=18; Figure 32). There was also a negative trend between centrality and Openness (r=-0.462, P=0.054, N=18). Centrality was not significantly related to either Sociability (r=0.441, P=0.067, N=18) or Attentiveness (r=0.088, P=0.727, N=18).

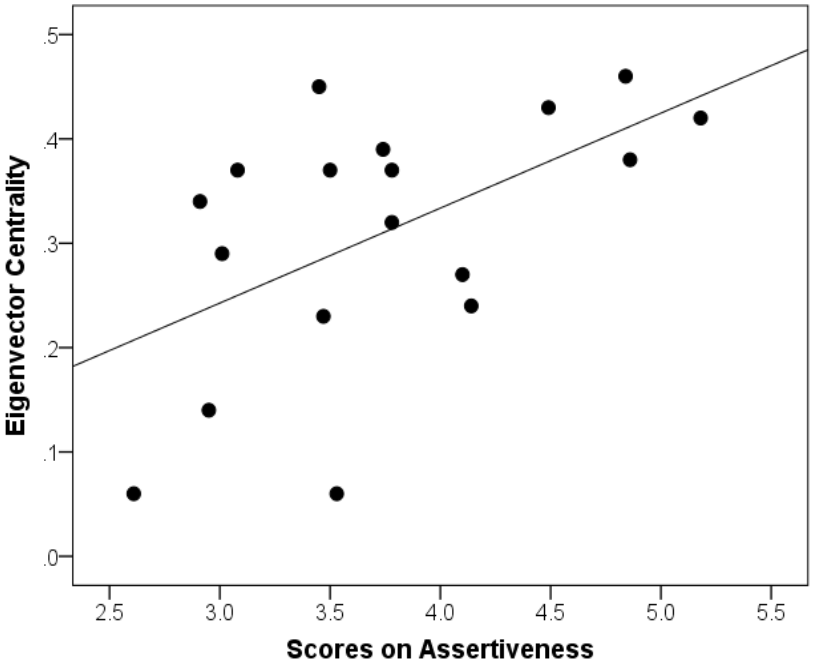


Figure 30. Relationship between individual differences in Assertiveness and social network centrality.

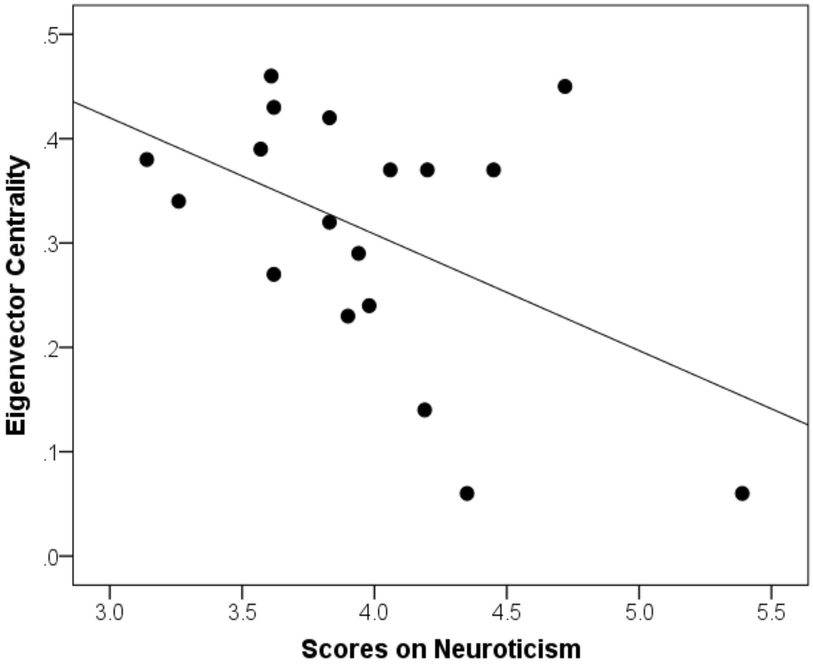


Figure 31. Relationship between individual differences in Neuroticism and social network centrality.

Controlling for all four basic social rules, none of the personality traits were significantly related to centrality although there was a trend between centrality and scores on Sociability (Assertiveness: r=0.292, P=0.311, df=12; Openness: r=-0.188, P=0.519, df=12; Neuroticism: r=-0.47, P=0.09, df=12; Sociability: r=0.524, P=0.054, df=12; Attentiveness: r=0.17, P=0.561, df=12). Controlling for social rank, Sociability was positively related to centrality (r=0.589, P=0.013, df=15; Figure 33) while the other personality traits were not significant (Assertiveness: r=-.22, P=0.395, df=15; Openness: r=-0.089, P=0.735, df=15; Neuroticism: r=-0.313, P=0.221, df=15; Attentiveness: r=0.06, P=0.818, df=15). When all basic social rules and personality traits were entered stepwise into a multiple regression model, social rank and Sociability were both significant predictors of centrality (AdjR2=0.549, F=11.341, P=0.001, df=17).

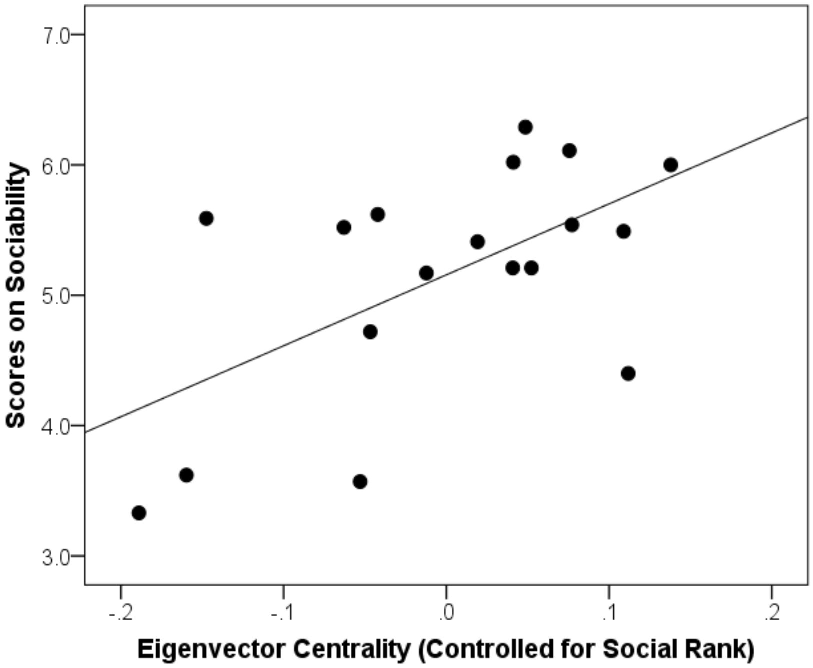


Figure 32. Relationship between social network centrality (controlled for social rank) and individual differences in Sociability.

6.4. Discussion

It was hypothesized that individual differences in the personality of capuchins at LL would be significantly related to differences in their social network position, and that these associations would be independent of any effects from basic social rules. Supporting the first hypothesis, without controlling for basic social rules, individual differences in Assertiveness were positively related to differences in monkeys' network centrality, while individual differences in Neuroticism were negatively related to centrality. After controlling for possible effects of basic social rules, individual differences in Sociability were found to be positively related to subjects' network centrality; however, these results were only significant if social rank was controlled for, and a multiple regression revealed that rank was the primary predictor of individual variance in centrality, followed by individual differences in Sociability. While these findings support the second hypothesis of this study, the results of the multiple regression suggest that individuals who are higher-ranking, and are *also* more Sociable, occupy more central positions within their group's social network.

The findings for Sociability reflect those reported in Chapter 3, which found that individual differences in this personality trait were positively related to differences in the amount of time subjects' spent in close proximity to others. The effects of social rank are similar to many behavioural studies on capuchins showing that higher-status monkeys are generally the most socially active and spatially embedded members of their group (Janson, 1990; Fragaszy et al. 2004; Tiddi et al. 2011). The results of this study also generally reflect those reported in Chapter 5, which found that Sociability and rank were both independent predictors of social relationship quality among these capuchins. The present study found a negative but non-significant trend between centrality and scores on Openness, which likely reflects the fact that similarities in

Openness were significantly correlated with scores on agonistic relationship quality (Chapter 5). Although this latter correlation was non-significant, the effect size was nevertheless moderate and the non-significance could be due to the relative small sample of monkeys in this analysis (N=18).

Monkeys that score high on Assertiveness are characterized as being more aggressive, bullying, and manipulative than others (Chapter 3). Individual scores on this personality trait have been shown to correlate positively with differences in social rank (Chapter 3). This association between Assertiveness and rank-related behaviour explains why scores on this personality trait were no longer significantly related to monkey's social network position after controlling for rank. As such, Assertiveness alone cannot explain social network structure beyond that explained by basic social rules, but it is possible that this personality trait underlies the social rank of these monkeys. There is tentative morphological evidence suggesting that Assertiveness in capuchins has an underlying hormonal component to it (possibly testosterone; Lefevre et al. 2014), which in turn may contribute to the behavioural tendencies necessary for individuals to acquire higher rank within their group.

Monkeys that score high on Neuroticism are generally more erratic, impulsive, and unstable compared to less-Neurotic individuals (Chapter 3). Previous work has shown that animals, including humans, who score highly on neurotic-like traits (e.g. timid/shy) may have a tendency to limit or avoid social situations (e.g. Asendorpf 1990; Pike et al. 2008; Aplin et al. 2013). This effect could explain why Neuroticism was inversely related to capuchins' network centrality. Highly Neurotic individuals may also have developed those traits over time due to having been ostracised to the periphery of the group by higher-status monkeys. Indeed, after controlling for rank, the relationship between Neuroticism and centrality was no longer significant, suggestive of some underlying interaction between higher Neuroticism and lower rank.

Although kinship, age, and sex were not significantly related to subjects' network centrality, such findings generally reflect the ambiguous role these basic social rules play within capuchin societies. For example, Schino et al. (2009) found adult female capuchins gave coalitionary support to kin over nonkin in all of the aggressive encounters that were recorded among their subjects. In contrast, Ferreira et al. (2006) reported that kinship did not influence the pattern of coalitionary behaviour within their population of capuchins; rather, rank had the greatest influence when younger monkeys were involved. Only through further research will we be able to better understand why basic social rules predict patterns of sociality in some cases, but not in others. If, as Janson (1990) suggests, spatial proximity among brown capuchins is influenced mostly by subordinates' avoidance of higher-ranking group members (e.g. to avoid conflict), then the lack of a sexual difference in network centrality among the LL capuchins could reflect the fact that males are not necessarily more aggressive than females (Fragaszy et al. 2004). It is also possible that the same factors influence network position in both males and females (e.g. push/pull of rank), resulting in sex having no significant effect on network centrality at LL.

As with previous studies of personality-network associations, the correlational nature of the results presented in this study make it impossible to define causality between personality and spatial network centrality. On the one hand, individuals with particular personality traits may actively seek social embeddedness within their groups. On the other hand, social embeddedness may itself shape the personality of individuals. Indeed, although personality is generally stable across time and contexts, these traits nevertheless can have an element of plasticity to them, particularly among younger individuals (Terracciano et al. 2006; Frost et al. 2007). Longitudinal data are therefore needed to further examine the issue of causality in personality-network associations.

6.5. Conclusions

It is clear from this analysis that individual differences in personality predict differences in the social structure of capuchins, and more importantly, certain traits of personality (i.e. Sociability) can explain network position beyond that explained by basic social rules alone. These findings highlight the importance of taking personality into consideration when examining what factors contribute to the social structure of animals, and raises intriguing questions about the possible selective advantages of personality in terms of how individuals become socially embedded within their networks.

CHAPTER 7

Individual Learning in Brown Capuchin Monkeys

Photograph 7

CHAPTER 7

Individual Learning in Brown Capuchin Monkeys

7.1. Introduction

Animals learn by acquiring new or modifying existing knowledge, behaviours, or skills through experience (Shettleworth 2009). Neurologically, learning occurs when new or existing connections are created or modified between two or more neurons (Sokolov 1977). Although these neural circuits are considerably complex in certain taxonomic groups (e.g. mammals), the mechanisms of learning are quite primitive. Indeed, learning has been documented in all animals studied to date, including unicellular organisms (Hennessey 1979; Fernando et al. 2009). Several studies have also shown that when animals' cerebral cortices are surgically removed, they are still capable of learning in some instances (Thompson and Donegan 1986; Thompson 1991). Thus, the site of learning perhaps exists within the cerebellum – an evolutionarily ancient region of the brain (Northcutt 2002).

The ability to adjust one's behaviour according to experience and changes within the environment can lead to fitness-related benefits, thereby favouring the evolution of learning through natural selection. Most fundamentally, animals need to learn to avoid danger and to acquire resources to survive and reproduce. For instance, patchiness of resources has been proposed to favour the evolution of learning in bees (*Apis cerana*), presumably because it enables them to locate food more efficiently (Krakauer and Rodriguez-Girones 1995). In Japanese quail (*Coturnix japonica*), Gutierrez and Domjan (1996) found that males who learned to anticipate the arrival of females had a mating advantage over others. Lastly, in blue gourami fish (*Trichogaster trichopterus*), Hollis (1984) and Hollis et al. (1995) found that males were more likely to win fights if they learned to anticipate and quickly react to such events beforehand.

Despite the benefits, there are also important costs to learning. In humans, for example, the process of learning a task can be energetically expensive (Haier et al. 1992). Additionally, the speed at which animals learn can determine how long they exhibit sub-optimal behaviour, which in turn may place constraints on their own fitness as well as those around them. For instance, offspring must learn how to survive on their own, and until then, they must remain dependent on their mothers, further delaying her future reproductive success (Shettleworth 2009).

7.1.1. Types of Learning

Multiple types of learning exist, all of which follow either non-associative or associative principles. Habituation, the most wide-spread form of learning in animals (Shettleworth 2009), is an example of non-associative learning whereby an individual exhibits a progressive decline in responding to a repeated stimulus to the point where they no longer react to it (Bouton 2007). For instance, a rat might initially react fearfully upon hearing a loud noise, but over time and with repeated exposure to the noise, the rat may begin to ignore the stimulus presumably because the rat no longer perceives the noise as an immediate threat. Sensitization is another example of non-associative learning whereby an individual progressively amplifies its response to a repeated stimulus (Shettleworth 2009). For example, repetition of a loud, painful noise may make a subject more responsive to the noise over time.

In contrast to non-associative forms of learning, associative learning is a process whereby an individual learns something via its association with a separate, usually pre-occurring, stimulus (Thorndike, 1931; Mitchell et al. 2009). Two of the best-studied forms of associative learning are classical (or “Pavlovian”) conditioning and operant (or “instrumental”) conditioning. In classical conditioning, a subject responds to a neutral stimulus as it would to another, non-neutral stimulus by learning to associate the two stimuli. Pavlov (1927) was the first to describe classical conditioning using dogs as study subjects. In these experiments, a tone would sound prior to feeding the dogs. Over time, the dogs would begin to salivate as soon as the tone was given, but prior to the appearance of food, suggesting they had come to associate the tone (a neutral stimulus) with food (a non-neutral stimulus). By contrast, operant conditioning is not completely passive and is dependent on the consequences of one’s behaviour through reinforcement and punishment, such as a bird learning to perfect its nest building skills so that it withstands high winds and heavy rain. Operant conditioning also differs from classical conditioning in that the subject must learn through trial-and-error how to operate on its environment to produce a desired result (e.g. retrieval of a food reward). Thorndike (1989, 1931) and Skinner (1953) were both instrumental to the study of operant conditioning. In particular, Thorndike (1931) proposed the “Law of Effect”, which predicts that animals will repeat behaviours that have positive outcomes (e.g. hunger satiation), while behaviours that result in negative outcomes (e.g. pain) will generally be avoided. This law later provided the framework for Skinner’s (1953) principles of operant conditioning, whereby an “operant” establishes the relationship between an animal’s behaviour and its environment, and the effect, or consequence, of an animal’s response influences its future rate of that response. For example, monkeys and birds are known to adopt a “win stay-lose shift” strategy to solve tasks whereby they will try the response that was last rewarded, and if that response is no longer rewarded, they will shift to another response (Nowak and Sigmund 199; Warren 1966; Shettleworth 2009).

Multiple studies have shown that individual differences in animals' performances on operant tasks from different domains (e.g. physical and social) are correlated; meaning, individuals that perform well on one particular task are likely to perform well on other tasks as well. For instance, in several studies of mice, a principle components analysis (PCA) identified a single factor which accounted for 38% of the total variance in subjects' performance on tasks measuring odour discrimination, spatial memory, associative fear conditioning, and operant avoidance (Matzel et al. 2003). In chimpanzees, Herrmann and Call (2012) found that a single factor accounted for as much as 68% of the variability in subjects' performance on three learning tasks designed to measure subjects' ability to discriminate between various colours, sizes, and shapes. Finally, in pigeons (*Columba livia*), Bouchard et al. (2007) found that performance on task measuring innovation (which requires individual learning) and social learning (i.e. learning by observing others) were positively correlated across subjects. These studies all suggest that individual differences in learning performance are driven by some underlying general learning factor across a variety of animal taxa.

7.1.2. Measuring Individual Differences in Learning

When measuring individual differences in learning, it is important to take into account whether subjects are motivated to engage in testing, whether they are paying attention during trials, and what level of prior experience they have with the task (Shettleworth 2009). If such factors are not taken into account, this can lead to difficulties with interpretations of task performance data. For example, individuals whose hunger has been satiated prior to testing may perform poorly on a task that uses positive reinforcement with food rewards (i.e. lack of motivation; Tolman and Honzik 1930), while subjects that pay closer attention on trials may perform better on a task compared to other individuals, but this does not necessarily mean they are better “learners” *per se* (Davis et al. 2001; Dalton and Behm 2007). Subjects that have prior experience operating a particular task may also take less time solving it than subjects with no prior experience (Shettleworth, 2009). For these reasons, researchers usually administer tasks to subjects individually within research cubicles, where it is possible to have better control over such variables.

Because unconditioned stimuli such as food or pain have pre-existing biological significance to animals, learning is usually easy to measure by observing subjects’ behaviour (Shettleworth 2009). For example, if subjects behave as if they expect an unconditioned stimulus following exposure to a conditioned stimulus (e.g. the tone used in Pavlov’s conditioning experiments), it is clear that some form of learning has occurred. Importantly, however, merely observing a change in behaviour is not diagnostic of learning (e.g. fatigue). Similarly, when something has been learned, it is not always apparent from the behaviour of the animal (e.g. learning how to perform a task by watching others solve it). Therefore, to understand what has or has not been learned on a given task, experiments must be designed such that they elicit a specific response in subjects that can then be used to monitor subjects’ learning progress (e.g. pressing down on a lever upon hearing a tone). For operant learning tasks, reinforcement from chance correct responses should eventually outweigh the effects of unreinforced trials (Thorndike 1931; Skinner 1953; Shettleworth 2009). These performance data can then be plotted as a “learning curve”, i.e. a graphical representation of the changing rate of learning on a task (Ebbinghaus 1885; Wozniak 1999). Theoretically, learning curves follow an “S-shape” pattern whereby a subject’s performance improves as they gain further experience and knowledge on how to solve the task, when then gradually evens out as the animal acquires less new information

(Shettleworth, 2009). Binomial tests are useful for determining when a subject's performance on a task has significantly risen to above chance levels (e.g. 80% correct responses on 12 trials) (e.g. Morton et al. 2013).

7.1.3. This Study

This chapter investigates individual differences in the associative learning abilities of two groups of brown capuchin monkeys housed at the "Living Links to Human Evolution" Research Centre, UK. Capuchins are renowned for their inquisitiveness, relatively large brains, and ability to solve complex tasks (Chapter 2). Capuchins have therefore been used in many studies on individual and social learning (Chapter 2).

Two operant tasks were administered to subjects individually within research cubicles under conditions of positive reinforcement (i.e. food rewards) and free-choice participation. To facilitate interpretations of subjects' learning performance, these data were examined in relation to individual differences in subjects' age (Elias and Elias 1976), attention span during testing (Shettleworth 2009; Morton et al. 2013), time spent scrounging within social groups (i.e. exploiting food acquired by others; Arbily et al. 2010), time spent feeding within subjects' main indoor/outdoor enclosures (Raine and Chittka 2008), and personality (i.e. individual differences in behavioural consistency across time and contexts; Gosling 2001; Carere and Locurto 2011). As noted previously, attention span during testing and food-related motivation are important variables which can affect subjects' learning on tasks (Shettleworth 2009). Additionally, previous work has reported correlations between age and learning, perhaps reflecting the long-term experience and problem-solving knowledge of subjects (Hebda-Bauer et al. 2005; Bailey et al. 2014), or interactions with developmental changes (Ramscar and Githcho 2007; Pattwell et al.

2012; van den Bos et al. 2012). Finally, a growing body of research suggests that individuals with particular personality traits (e.g. exploration and boldness) are more likely to perform well on tasks as a result of their general inquisitiveness and lack of fear towards novel situations (Morton et al. 2013). For instance, slow-exploring guppies are often better spatial navigators (Burns and Rodd 2008), and less neophobic birds have a tendency to be faster learners (Boogert et al. 2006). Because personality is generally stable over time and across contexts (Chapter 3), interactions between personality and performance on tasks likely persist across multiple tests or phases of experiments, thus giving the illusion of some subjects being consistently "smarter" than others (Herrmann and Call 2012). Collectively, these analyses will be used to understand individual variability in the task performance of capuchins at Living Links.

7.2. Methods and Materials

7.2.1. Learning Tasks

Subjects underwent testing on two operant tasks between 8 November 2010 and 1 April 2011, at 12 trials per session, four sessions per week. Chapter 2 describes each task and methods of administration in detail. All group members (N = 18 monkeys, excluding infants) were given the opportunity to engage in testing (i.e. "free choice" participation). Subjects' learning performance was calculated per task by dividing the total number of trials answered correctly by the total number of trials undergone, multiplied by 100. An increase in performance over time indicated subjects were progressively learning each task (Shettleworth 2009). Individuals who scored $\geq$80 % on three consecutive sessions met learning criteria. Performance scores were averaged across tasks to yield an average performance score. Subjects were given food rewards during trials to encourage participation, motivation, and attention during testing. Finally, free-choice participation was used to further ensure that those individuals that participated were sufficiently comfortable and motivated to engage in testing. Average participation was calculated by dividing the number of trials a subject participated by the total number of trials offered to that individual, multiplied by 100.

7.2.2. Behavioural Sampling

Fifty-four hours of focal observations were recorded between May and August, 2011, totalling 3 hours per individual. All behaviours (Chapter 2) were recorded daily per focal monkey for 10 minutes. Monkeys were sampled evenly between 9:00 and 17:30. Incidences of scrounging were recorded continuously and represented in terms of the total number of events recorded. Feeding behaviour was recorded at 1-min intervals using point sampling methods and is represented in terms of the total percept of observation time in which subjects were engaged in this behaviour (Martin and Bateson 2007).

7.2.3. Attention Span During Testing

During testing, subjects were scored once per trial on a 3-point scale according to whether they exhibited high (3), medium (2), or low (1) attention. Attention was based on how often they looked away during testing. Mean scores were calculated per monkey across trials. Inter-observer reliability tests were satisfactorily concordant (Chapter 2). Further details on these methods can be found in Chapter 2.

7.2.4. Personality

Data on subjects' personalities come from Chapter 3. Five distinct personality traits were reliably demonstrated and behaviourally validated in a large sample (N=127 subjects from 7 sites) of brown capuchin monkeys: Assertiveness (e.g. *aggressive*, *bullying*), Openness (e.g. *curious, active*), Attentiveness (e.g. *organized*, *perceptive*), Neuroticism (e.g. *excitable, erratic*), and Sociability (e.g. *affectionate*, *friendly*). Subjects' scores per trait were calculated and used in this study.

7.2.5. Statistical Analyses

Pearson correlations tested relationships between variables. Partial correlations controlled for variables. Monkeys that regularly participated on both tasks (>50% of trials) were used to examine relationships between average task performance and individual differences in subjects' age, personality, feeding time, scrounging, and attention span. All analyses were conducted using IBM SPSS Statistics 19.

7.3. Results

7.3.1. Task Participation and Performance

Thirteen monkeys participated in Task 1 and participated on an average of 78.3 ± 26.6% of sessions (range: 10-100%). One of these subjects participated in <50% of sessions, 5 subjects participated in 100% of sessions, and the remaining subjects participated somewhere in between 50-100%. Each participant received between 11-120 trials (mean: 75.15 ± 25.17 trials) over the course of the task, which was a function of how many sessions in which they participated (Table 22). Average performance among participants was 74.04 ± 15.59% (range: 45.5-92.8%). A total of eight monkeys learned the task within 54-86 trials (mean performance: 83.43 ± 4.8%), which was faster than the 5 remaining monkeys who were still performing at chance levels by the end of the task (mean performance: 59.03 ± 15.18%). Subjects' learning curves on this task are provided in Figure 34.

Table 24. Summary of results for each monkey for Task 1 and Task 2.

Participant	N Trials Administered		Average Performance Across Sessions (%)		Learning Criteria Met?	
	Task 1	*Task 2*	*Task 1*	*Task 2*	*Task 1*	*Task 2*
Anita	87	193	52.9	59.1	---	---
Carlos	69	84	78.8	77.4	Yes	Yes
Chico	54	97	92.8	79.3	Yes	Yes
Diego	---	120	---	54.17	---	---
Figo	95	193	77.8	59.0	---	---
Inti	64	240	72.7	51.7	---	---
Junon	86	228	77.5	67.2	Yes	---
Kato	80	48	86.2	86.7	Yes	Yes
Lana	11	12	45.5**	41.7**	---	---
Manuel	---*	66	---	71.1	---	---
Micoe	76	169	84.1	59.2	Yes	---
Pedra	83	60	84.7	81.7	Yes	Yes
Penelope	---*	46	---	67.63	---	---
Popeye	120	---*	46.29	---	---	---
Santi	68	24	80.51	50.0	Yes	---
Sylvie	84	48	82.8	77.1	Yes	Yes

*= monkey did not participate in the task; **=monkey participated only on one session.

Subjects that participated >50% on all trials are highlighted in bold.

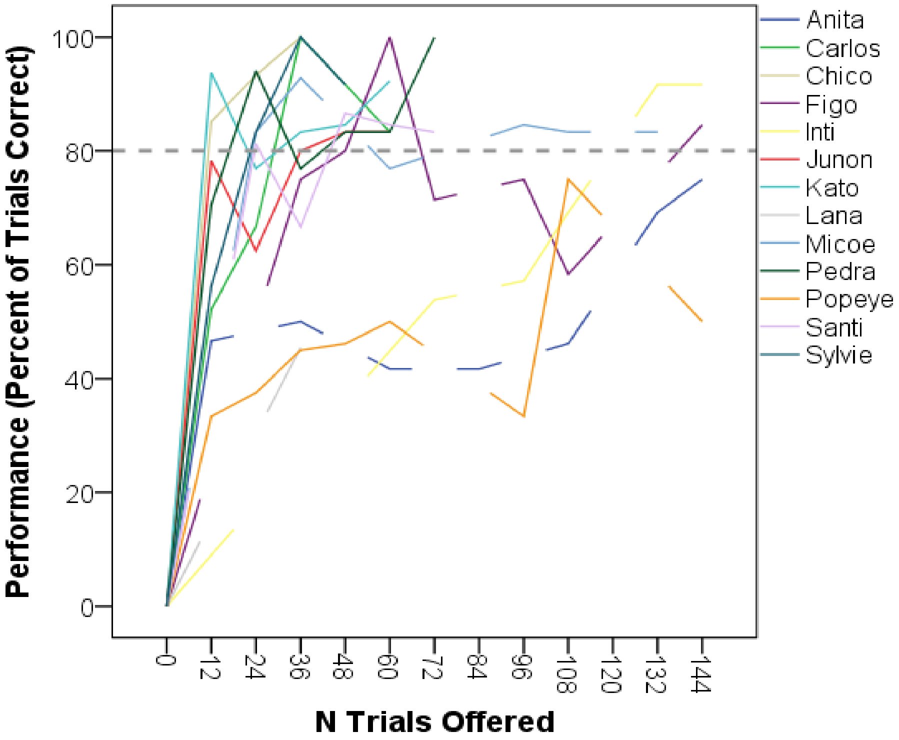


Figure 33. Performance curves for each participant in Task 1. Gaps in the performance curve of a given participant indicate they did not participate during those sessions despite being offered the opportunity to engage. Participants received 12 trials per session per day until they met learning criteria (≥80% trials correct for three consecutive sessions). The grey dotted line on the graph was used as a reference to indicate where monkeys were performing >80% on any given session.

Fifteen monkeys participated in Task 2 and participated in an average of 69.3 ± 36.8% sessions (range: 4.8-100%). Five of these subjects participated in <50% of sessions, 6 subjects participated in 100%, and the remaining subjects participated somewhere in between 50-100%. Participants received between12-240 trials (mean: 108.5 ± 76.63 trials) which was a function of how many sessions in which they participated (Table 22). Average performance among individuals was 65.52 ± 13.3% (41.7-86.7%). Five monkeys learned the task within 48-97 trials (mean performance: 80.41 ± 3.95%), which was faster than the 10 remaining monkeys, who, as in Task 1, were still performing at chance levels by the end of the task (mean performance: 58.1 ± 9.1%). Subjects' learning curves on this task are provided in Figure 35.

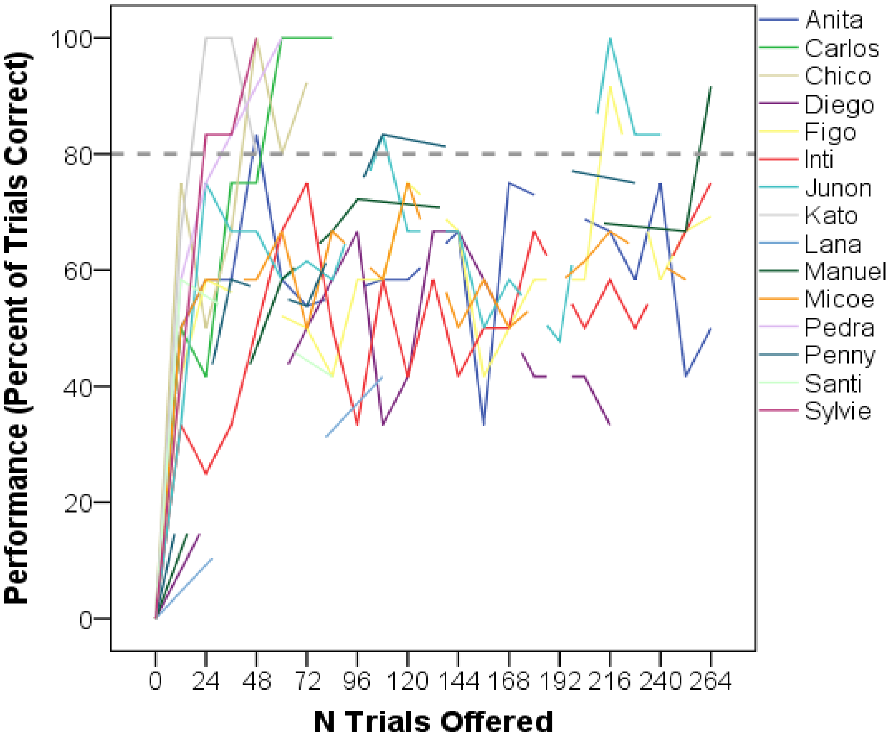


Figure 34. Performance curves for each participant in Task 2. Gaps in the performance curve of a given participant indicate they did not participate during those sessions despite being offered the opportunity to engage. Participants received 12 trials per session per day until they met learning criteria (≥80% trials correct for three consecutive sessions). The grey dotted line on the graph is used as a reference to indicate where monkeys were performing >80% on any given session.

7.3.2. Factors Related to Task Performance Variability

Task performance was unrelated to scrounging (r=-0.535, P=0.111, N=10), age (r=-0.434, P=0.211, N=10), attention span during testing (r=0.302, P=0.396, N=10), and time spent feeding within main enclosures (r=0.155, P=0.669, N=10). Task performance was negatively related to Assertiveness (r=-0.67, P=0.036, N=10; Figure 36), but unrelated to the other personality traits (Openness: r=0.447, P=0.195, N=10; Neuroticism: r=0.47, P=0.17, N=10; Sociability: r=0.359, P=0.309, N=10; Attentiveness: r=0.034, P=0.926, N=10).

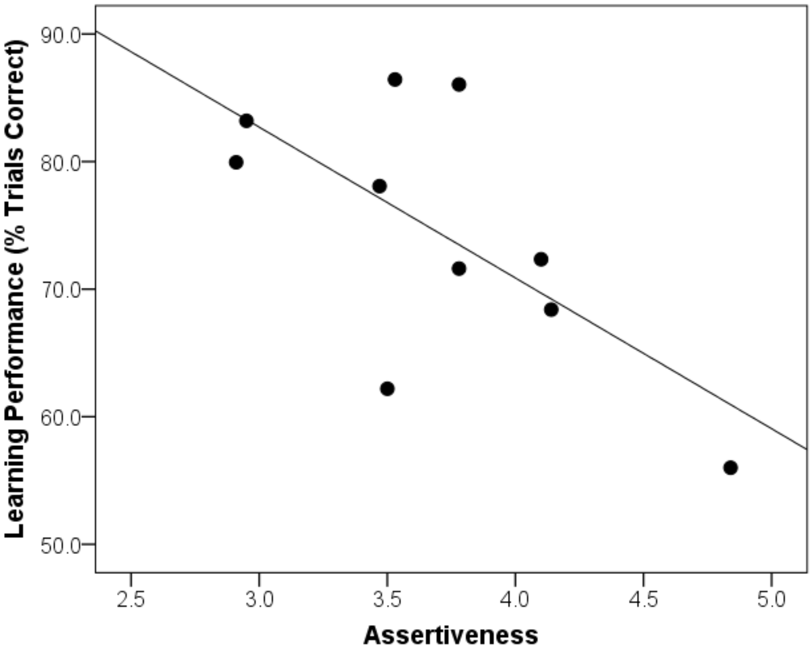


Figure 35. Relationship between learning performance and subjects’ scores on Assertiveness.

7.4. Discussion

This chapter aimed to investigate the associative learning abilities of the Living Links capuchins monkeys by testing subjects on two operant tasks, which were administered individually to each monkey within research cubicles under conditions of positive reinforcement (i.e. food rewards) and free-choice participation. Eighteen monkeys were given the opportunity to participate in tasks; however, only ten of these subjects were regular participants. To facilitate interpretations of regular participants’ performance on tasks, individual differences in their average task performance were correlated with a range of variables that could potentially influence subjects' performance on the tasks.

Regular participants showed considerable variation in their average performance on tasks (Table 22). Task performance was unrelated to individual differences in attention span, suggesting that subjects were attentive and sufficiently motivated during trials. Indeed, subjects were given food rewards throughout testing to encourage motivation and attention (see "Methods and Materials"), and free-choice participation was used to further ensure that individuals who participated regularly on tasks would be sufficiently comfortable and motivated to engage in testing. Thus, attention span cannot explain why some monkeys performed better than others on these tasks. Average task performance was also not significantly related to individual differences in the amount of time subjects spent feeding within their main indoor/outdoor enclosure, nor the number of times they engaged in scrounging within their social groups. These findings suggest that subjects were not necessarily participating in this study because they sought out food due to hunger or merely because it was an easy source of food (i.e. a "hand-out"). As described in Chapter 2, the capuchins at Living Links are provided with ample food three times daily, with occasional scatter feeds inserted between these time periods. Therefore, it seems unlikely that subjects who performed well on tasks did so because they were motivated by hunger or hand-outs. Finally, task performance was unrelated to individual differences in task participation, indicating that prior experience with the tasks could not explain why some individuals performed better than others.

Individual differences in Assertiveness were negatively correlated with average task performance. Several authors have proposed that individuals with aggressive personality traits emphasize speed over accuracy in their general decision-making, which in turn may influence their performance on tasks (reviewed in Sih and Del Giudice 2012). In the present study, the association between performance and Assertiveness supports such predictions. Firstly, Assertiveness was characterised by items like *aggressive*, *bullying*, and *dominant* (Chapter 3), and monkeys' scores on this personality trait were positively correlated with the amount of time monkeys spent being aggressive towards others (Chapter 3). Secondly, individual differences in performance were negatively associated with scores on Assertiveness; meaning that less Assertive individuals were solving the tasks faster than more Assertive monkeys. However, because Assertiveness was also positively associated with the amount of time monkeys spent socializing amongst themselves (Chapter 3), it is equally possible that highly-Assertive individuals simply performed poorly on tasks because they gave priority to remaining within their social groups versus being isolated within research cubicles for testing. Regardless of the underlying reason(s), in light of the fact that personality reflects individuals' behavioural consistency across time and contexts (Gosling 2001), the performance data obtained from the present study are not necessarily reflective of individual differences in monkeys' learning capacity *per se*, but rather their willingness to *apply* those skills to solve tasks in general (Morton et al. 2013).

None of the other personality dimensions (Openness, Sociability, Neuroticism, and Attentiveness) were related to performance. Given that these dimensions are related to other aspects of subjects' behavior (e.g. scores on Openness are positively associated with the amount of time monkeys play with others; Chapter 3), the traits associated with Assertiveness may be particularly relevant to performance within this capuchin population. However, further work will be necessary to determine causal relationships among these variables. For instance, familiarity (and thus lack of fear) with the experimenter and/or research environment could underlie why individual differences in performance were not significantly associated with scores on Neuroticism, a trait characterized by erratic and excitable tendencies (Chapter 3).

7.5. Conclusions

D'Amato and Salmon (1984, p.164) poignantly stated that "during 17 years of research with [capuchin] monkeys we have alternated between marvelling at their cognitive accomplishment and being plunged to the depths of despair over their inability or reluctance to learn a variety of apparently simple tasks". Based on findings from the present study, it is possible that individual differences in personality impacts the task performance of capuchins, explaining why individuals may perform well on some tasks, but poorly on others.

Scores on regular participants' task performance will be used to test hypotheses relating to individual differences in capuchins' learning performance and social success in Chapter 8; these hypotheses will be tested with and without controlling for individual differences in Assertiveness.

CHAPTER 8

Individual Learning and Social Success in Brown Capuchin Monkeys

Photograph 8

CHAPTER 8

Individual Learning and Social Success in Brown Capuchin Monkeys

8.1. Introduction

Cognitive and learning performance, i.e. "intelligence" (Neisser et al. 1996), is one of the hallmarks of the primate lineage. According to the Social Intelligence Hypothesis (SIH), such abilities evolved in order to manage the diversity and intensity of primates' social environment (Byrne and Whiten 1988; Dunbar 1998). In particular, as group-living became more socially demanding, primates presumably became more reliant on strategies such as cooperation, deception, and acquiring knowledge about others to achieve social success within their groups (Byrne and Whiten 1998). Social success, defined here in terms of the content and quality of social relationships formed between group members (i.e. "social embeddedness"; Whitehead 2009), is related to lower levels of stress, longer life span, greater access to food and mates, reduced exposure to predators, and greater social support from others (Abbott et al. 2003; Fragaszy et al. 2004; Schulke et al. 2010; Silk et al. 2010; Fichtel 2012). Thus, evolving the mental capacity to solve social challenges and achieve greater success within groups likely enabled primates to improve their survival and reproductive fitness (e.g. Pawlowski et al. 1998).

Phylogenetic analyses show that species differences in primate group size, grooming clique size, social organization, rates of coalitionary support, and rates of tactical deception (all proxy measures of social complexity) are positively associated with species differences in intelligence (e.g. relative brain size and performance on cognitive tasks; Byrne and Corp 2004; Dunbar and Shultz 2006; Amici et al. 2008; Lehmann and Dunbar 2009). To date, however, few studies have examined how individual differences in primate intelligence (as defined in terms of performance on cognitive/learning tasks) are associated with differences in social success, which remains critical to understanding how intelligence evolves at higher taxonomic levels.

Humphrey (1976; p. 311) proposed that "if intellectual prowess is correlated with social success, and if social success means high biological fitness, then any heritable trait which increases the ability of an individual to outwit his fellows will soon spread through the gene pool...to increase the general intellectual standing of the species". Supporting this argument, primates use social knowledge to improve their status within groups (Byrne and Whiten 1988), and individuals with larger relative brain sizes exhibit larger social networks (Sallet et al. 2011; Powell et al. 2012). Nevertheless, behavioural observations are not a reliable measure of individual differences in intelligence *per se* (e.g. Drea and Wallen 1999). Moreover, the extent to which brain size reflects intelligence, particularly at the individual level, remains controversial (e.g. Healy and Rowe 2007). Thus, data on cognitive and learning task performance, which can be administered to individuals under carefully controlled conditions, may provide a more direct approach to testing the SIH at the individual level.

Learning contingencies are likely to be complex in primate societies, and much of primates' socially intelligent behaviour can often be explained through simple associative rules (Barrett et al. 2007). Indeed, acquiring skills to deceive others, classifying conspecifics according to kinship and rank, recalling third-party relationships, and gauging whether individuals are likely to cooperate versus defect based on prior interactions all require an efficient capacity to learn and remember (Barrett et al. 2007; Byrne 1997). Therefore, better learners should be more socially successful than poorer learners as a result of their ability to learn how to solve social challenges. Data on individual learning in primates, however, do not support this prediction. In several macaque species (e.g. *Macaca fascicularis*, refs; *Macaca nemestrina*, Strayer 1976; Bunnell et al. 1980; Bunnell and Perkins 1980) and ring-tailed lemurs (*Lemur catta*; Kendal et al. 2010*)*, individual differences in performance are inversely related to social rank (a proxy measure of social success; Silk et al. 2006). Thus, contrary to what the SIH might predict at the individual level, better-learning primates may be *less* socially successful than poorer learners.

Several issues, however, warrant consideration. First, learning variance may reflect differences in subjects' willingness to engage in research. Indeed, Chapter 7 discussed how individuals that performed worse on learning tasks were also the most sociable individuals within their groups, suggesting perhaps that these individuals lacked motivation because they prioritized remaining within their groups over engaging in research conducted in isolation (e.g. research cubicles). Second, if social success is defined in terms of social embeddedness, then social status may only be an indicator of social success rather than a determinant. Indeed, other factors are known to contribute to the social success of primates (e.g. sex, kinship, personality, and friendships; Silk 2002; Chapters 5 and 6). Thus, it remains necessary to test the association between learning and social success using an actual measure of social embeddedness (e.g. social network analysis; Whitehead 2008). Third, better learners may be able to improve their status over time by directing affiliative behaviour towards individuals more socially successful than themselves (i.e. "Machiavellian" behaviour, Byrne and Whiten 1988; or "grooming up the hierarchy", Seyfarth 1977), yet given the relatively rigid hierarchical and nepotistic social organization of the primates used in previous studies of learning and social rank (particularly rhesus macaques; Thierry et al. 2008), better learners may have avoided attempting to use affiliative strategies to improve their social status due to the costs of status conflicts (e.g. physical aggression; Drea and Wallen 1999). Thus, a stronger and more positive correlation between learning and social success may exist among species that are relatively more socially relaxed.

The relationship between individual learning performance and social success was investigated within two captive groups of capuchin monkeys housed at the “Living Links to Human Evolution” Research Centre, UK. Capuchins are of particular interest given their relatively large brains, complex learning abilities, and socially intelligent behaviour (Chapter 2). Moreover, compared to many old world primates, particularly rhesus macaques, capuchins are relatively more tolerant of the close proximity of others (including non-kin and particularly infants) and generally exhibit lower rates of agonism (Chapter 2). Capuchins therefore potentially have greater flexibility in their choice of social partners compared to less socially tolerant species, which may provide learners with more opportunities to improve their status over time.

Subjects’ average learning performance was measured on two operant tasks administered individually within research cubicles. Performance was then compared with social success (i.e. social network centrality) and the amount of affiliative behaviour subjects initiated with others. Based on the SIH, learning performance was predicted to be positively related to social success (Hypothesis 1) and the amount of affiliative behaviour subjects initiated with others (Hypothesis 2). Compared to poorer performers, better performers were also expected to seek greater social success by directing affiliative behaviour towards monkeys more socially successful than themselves (Hypothesis 3).

8.2. Methods and Materials

8.2.1. Learning Tasks

Subjects underwent testing on two operant tasks between 8 November 2010 and 1 April 2011, at 12 trials per session, four sessions per week. Chapter 2 describes each task and methods of administration in detail. Briefly, all group members (N = 18 monkeys, excluding infants) were given the opportunity to engage in testing (i.e. “free choice” participation). Subjects’ learning performance was calculated per task by dividing the total number of trials answered correctly by the total number of trials undergone, multiplied by 100. An increase in performance over time indicated subjects were progressively learning each task (Shettleworth 2009). Individuals who scored ≥80 % on three consecutive sessions met learning criteria. Performance scores were averaged across tasks to yield an average performance score. Subjects were given food rewards during trials to encourage participation, motivation, and attention during testing. Finally, free-choice participation was used to further ensure that those individuals that participated were sufficiently comfortable and motivated to engage in testing. Learning performance was not affected by individual differences in age, attention span, time spent feeding within main enclosures, amounts of scrounging off others, or four personality traits (Openness, Neuroticism, Sociability, and Attentiveness) (Chapter 7); however, learning performance was significantly related to individual differences in subjects’ scores on Assertiveness – a personality trait characterized by aggressive, bullying, and manipulative behaviours (Chapter 3 and 7). Therefore, all analyses involving task performance data were examined with and without controlling for Assertiveness.

8.2.2. Behavioural Sampling

Fifty-four hours of focal observations were recorded between May and August, 2011, totalling 3 hours per individual. All behaviours (Chapter 2) were recorded daily per focal monkey for 10 minutes. Monkeys were sampled evenly between 9:00 and 17:30. Incidences of aggression, coalitions, scrounging, and food sharing were recorded continuously; all other behaviours were recorded at 1-min intervals using point sampling methods (Martin and Bateson 2007). In each point sample, group members within two body lengths from the focal were recorded.

Capuchins engage in grooming, food sharing, and coalitions to establish and maintain relationships (Chapter 2). Therefore, the total number of such affiliative acts that subjects initiated with other monkeys was used to test Hypothesis 2. Data on grooming, i.e. behavioural "states", were subjected to a log survivorship analysis to determine how many "events" of grooming existed within the dataset (following Martin and Bateson 2007); grooming bouts separated by four minutes were considered independent events (Figure 1 in Appendix). To test Hypothesis 3, the number of affiliative acts that subjects initiated with more successful individuals minus the number they initiated with less successful individuals, divided by the total number initiated with all individuals regardless of their social success was calculated (hereafter "success symmetry").

8.2.3. Basic Social Rules

Basic social rules (i.e. age, sex, kinship, and social rank) are often predictors of social success in primates, including capuchins (Chapter 5). Effects from basic social rules may therefore possibly confound associations between social success and learning performance. For example, learning might appear to be associated with social success if better learners also happened to be those individuals with more relatives in their group. To remove these potential confounds, associations were tested between performance data and subjects' age (in years), sex, social rank, and mean coefficient of relatedness with others in the group (hereafter "kinship").

David's Scores were calculated using data on the win/loss outcomes of agonistic interactions; the following formula was used: DS = $w + w2 - l - l2$ (Gammell et al. 2003; David 1988). Details of this analysis can be found in Chapter 2. Monkeys' individual scores are provided in Tables 6 and 8 in the Appendix.

Each monkey's average coefficient of relatedness (r), or "kinship", with others in their group was estimated through pedigrees, whereby r=0.5 for parent-offspring relations, r=0.5 for full sibling relations, r=0.375 for ¾ siblings (e.g. cases of inbreeding), r=0.25 for grandparent-grandchild relations, r=0.25 for aunt/uncle-nephew/nice relations, r=0.125 for half siblings, and r=0.125 for first cousins.

8.2.4. Social Network Analysis

In wild and captive capuchins, individuals who spend more time in close proximity are less likely to engage in conflict and more likely to engage in affiliative behaviour (Chapter 2). This notion was validated within the LL population in Chapter 6. Therefore, data on subjects' spatial proximities with other monkeys were used as an index of social success; subjects with higher centrality (i.e. "spatial embeddedness") were considered more socially successful. The social network structures derived from the East and West spatial proximity datasets were considered robust (discussed in Chapter 6). Monkeys' scores on centrality are presented in Table 18 of the Appendix.

8.2.5. Statistical Analyses

Pearson correlations tested relationships between variables. Partial correlations controlled for variables. Analyses were conducted using IBM SPSS Statistics 19. Social networks were analysed in SOCPROG 2.4 (Whitehead 2009). Further details on the social network analysis are provided in Chapter 2 and Chapter 6.

8.3. Results

8.3.1. Does learning performance predict social success?

Task performance was negatively related to rank (r=-0.774, P=0.009, N=10) and network centrality (r=-0.639, P=0.047, N=10) (Figure 37). Controlling for Assertiveness, performance was no longer related to rank (r=-0.609, P=0.082, df=7) or centrality (r=-0.501, P=0.17, df=7).

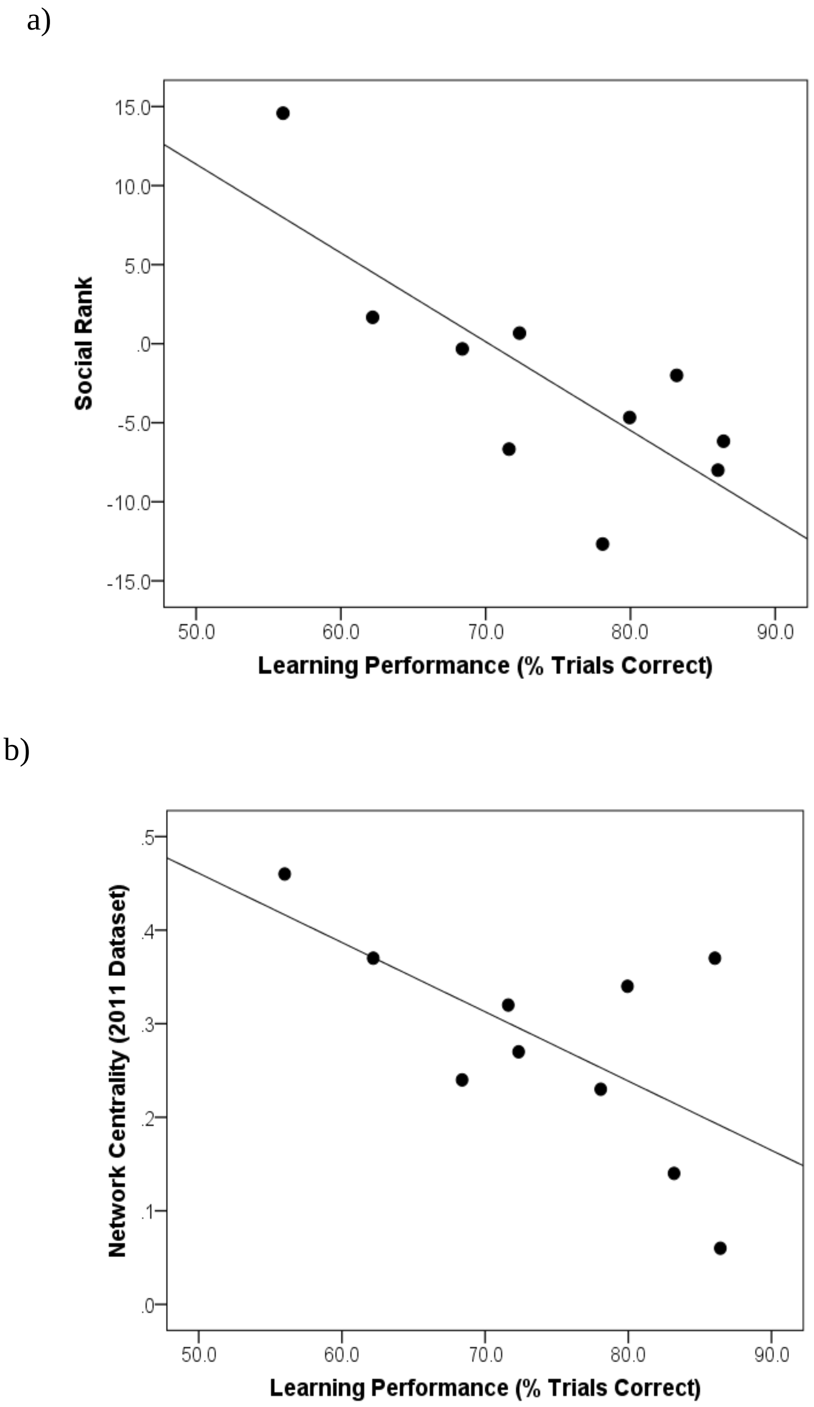


Figure 36. Relationships between task performance and a) social rank and b) social network centrality.

8.3.2. Do better learners seek social success?

Task performance was unrelated to success symmetry (r=0.273, P=0.445, N=10). Performance was negatively related to the number of affiliative acts subjects gave to others regardless of the recipient's social success (r=-0.637, P=0.047, N=10; Figure 38); controlling for Assertiveness, this effect was non-significant (r=-0.484, P=0.186, df=7).

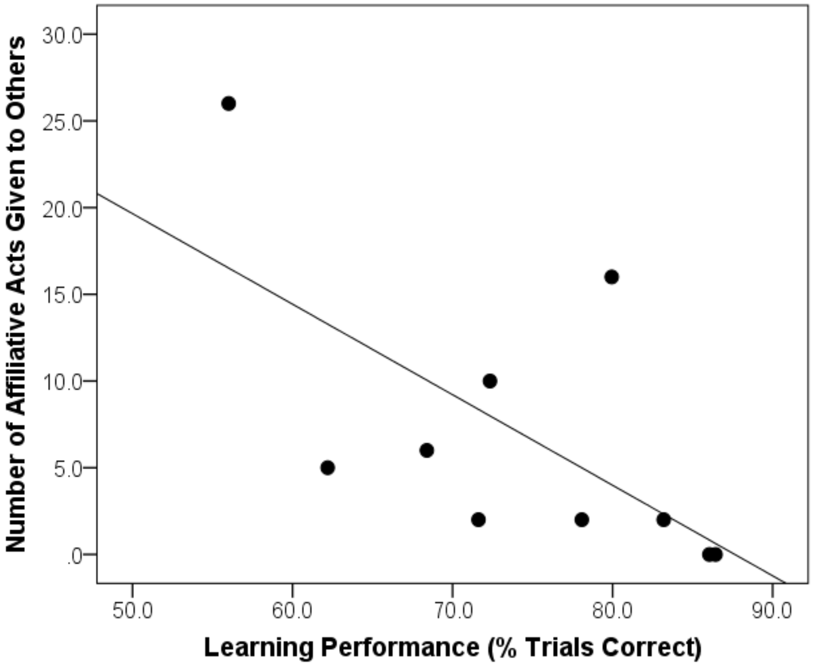


Figure 37. Relationship between learning performance and the number of affiliative acts subjects gave to others regardless of the recipient's social success.

8.4. Discussion

Task performance was negatively related to social rank and network centrality. Thus, in contrast to Hypothesis 1, better learners were less socially successful than poorer learners at the time of testing. Task performance was negatively related to the total number of affiliative acts subjects gave to others regardless of the recipient's social success. Better performers were also no more or less likely than poorer learners to seek affiliation with others more socially successful than themselves. Thus, in contrast to Hypotheses 2 and 3, better learners did not seek more opportunities than poorer learners to improve their social success.

These results are unlikely to reflect subjects' willingness to perform tasks when tested away from the group (i.e. in research cubicles), nor are they likely to reflect performance simply on physical-domain tasks. First, recent research on primates and other taxa have found no significant differences in subjects' task performance when housed in laboratory versus naturalistic settings, suggesting environment has little influence on task performance (Gazes et al. 2012; Krasheninnikova and Schneider 2014). Second, in both wild and captive primates, behavioural innovation within the physical and social domain (e.g. tool use and tactical deception), which requires individual learning, is observed more often among subordinates (e.g. Reader and Laland 2001; Wheeler 2009). Third, task performance among these capuchins is associated with individual differences in personality, reflecting subjects' general decision-making strategies (Chapter 7; Carere and Locurto 201; Morton et al. 2013). Lastly, multiple studies support the existence of a general learning ability in animals, including primates (e.g. Reader and Laland 2002; Matzel et al. 2003; Herrmann and Call 2012; discussed in Chapters 2 and 7). Thus, within this population of capuchins, better learners appear to occupy *less* socially successful niches within their groups compared to poorer learners.

8.4.1. Why are better learners less socially successful?

In macaques, Bunnell and Perkins (1980) noted that an increase in social rank resulted in a decrease in learning performance, suggesting that both variables were linked. Among the LL capuchins, individual differences in Assertiveness were positively related to differences in rank, aggressiveness, and social embeddedness (Chapter 3 and 6). In the present study, after controlling for Assertiveness, there was no longer a significant relationship between task performance and rank/centrality at the time of testing, suggesting this personality trait might mediate relationships between learning and social success.

In general, stronger competitors are expected to monopolize access to desirable resources (e.g. food, mates), forcing weaker competitors to innovate (e.g. Reader and Laland 2001; see also Chapter 1). Among the study subjects, higher-ranking capuchins may occupy a different behavioural niche whereby personality and brawn, but not brains, are incorporated into favourable behavioural strategies for achieving social success. If so, then as discussed in Chapter 7, performance on learning tasks may not necessarily reflect subjects' learning capacity *per se*, but rather subjects' willingness to apply their learning skills to solve tasks *in general*. Additionally, as discussed in Chapter 7, studies across numerous taxa show individuals with bolder and more aggressive personalities tend to emphasise speed over accuracy when making decisions, which may limit their task performance (i.e. "hasty decision-making"; Sih and del Giudice 2012). Thus, the results of the present study could reflect differences in the problem-solving strategies of less Assertive versus more Assertive individuals. Finally, although subordinate capuchins were better at learning alone inside research cubicles, they may have been unable to use those skills to solve social challenges within their group due to "inflexibility" of their social status. For instance, higher-ranking capuchins are typically the most socially active

(Chapter 3 and 6), and lower-ranking individuals (particularly males) are often ostracised to the periphery of their groups due to intolerance from alpha males (Janson 1990; discussed further in Chapter 6). These behavioural tendencies may explain why learning performance was negatively related to social success as well as the amount of affiliative acts subjects gave to others.

None of the scenarios outlined above are mutually exclusive *per se*. Regardless of underlying causality, however, if assertive personality traits played an important role in the evolution of primate intelligence, such interactions should also be evident at the species level whereby less assertive species exhibit greater intelligence compared to other species. Indeed, socially tolerant primates have a tendency to outperform less tolerant species on a range of problem-solving tasks (Moll and Tomasello, 2007; Herrmann et al. 2010; Amici et al. 2012). For example, bonobos perform better on tasks involving ‘theory of mind’, while chimpanzees perform better on tasks involving tool use (Herrmann et al. 2010). Although such differences in task performance may reflect species differences in cognitive skill, Herrmann et al. (2010) point out that the relatively greater social tolerance and passive coping style of bonobos could also be an important contributing factor.

8.5. Future Directions

Several issues warrant further investigation. In particular, although in the present study social success was defined in terms of rank and social embeddedness, future studies should consider alternative approaches to measuring social success, particularly reproductive success (Pawlowski et al. 1998). Secondly, while instances of socially intelligent behaviour among primates can often be explained more parsimoniously through simple learning contingencies (Barrett et al. 2007), further tests should be conducted within the cognitive domain (e.g.

transitive inference and meta-cognitive abilities; Call and Tomasello 1997) since such abilities may underlie social decision-making strategies in at least more cognitively advanced primate species (e.g. chimpanzees; Deaner et al. 2006; Call and Tomasello 2008; Amici et al. 2008). Finally, in contrast to studies on task performance in primates, studies on wild and captive birds have shown that task performance is *positively* related to individual differences in social rank (e.g. starlings [*Sturnus vulgaris*], Boogert et al. 2006), which is consistent with social intelligence ideas, whereas other studies have reported a negative or non-significant relationship between rank and learning (e.g. domestic chickens, Candland and Conklyn 1968; great tits [*Parus major*], Cole and Quinn 2011). Although the extent to which the SIH applies to non-primate taxa remains questionable (Beauchamp and Fernandez-Juricic 2004; Holekamp 2006; Shultz and Dunbar 2007), further research is needed to understand why such differences might exist between taxa, particularly in terms of aggressiveness, dominance expression, group cohesiveness, and the costs and benefits of individual learning.

8.6. Conclusions

Compared to poorer learners, better learners appear to be less socially successful. Additionally, the relationship between individual differences in learning and social success may be mediated by personality. As discussed, such findings do not support the hypothesis that better learners are concurrently the most socially successful individuals within their group, and instead are more supportive of hypotheses pertaining to behavioural innovation, “hasty decision-making” strategies, and/or social inflexibility.

CHAPTER 9

General Discussion

Photograph 9

CHAPTER 9

General Discussion and Conclusions

Given the diversity and intensity of social interactions that occur within primate societies, the learning contingencies faced by status-seeking group members are likely to be complex (discussed in Chapters 1 and 8). This thesis examined three hypotheses regarding the relationships between individual differences in primates' learning performance and social success (defined in this thesis in terms of social rank and social network centrality; discussed in Chapters 1 and 8). First, based on the Social Intelligence Hypothesis (SIH), it was predicted that individual differences in learning performance would be positively related to social success. In contrast, based on studies of behavioural innovation among animals, it was predicted that individual differences in learning performance would be inversely related to social success, since poorer competitors are expected to be more reliant on innovative strategies to gain access to desirable resources. Finally, based on studies of animal personality, it was predicted that learning performance would not be directly related to social success; rather, individual differences in personality should mediate this relationship. These predictions were tested within a captive population of brown capuchin monkeys, a species known for its advanced learning abilities, complex social behaviour, and social intelligence (discussed in Chapter 2).

In Chapter 3, five personality dimensions were identified and validated within a large multi-site sample of brown capuchins. These traits were labelled Assertiveness (e.g. aggressive, bullying, manipulative), Openness (e.g. curious, active, playful), Sociability (e.g. friendly, sociable, affectionate), Neuroticism (e.g. erratic, unpredictable, impulsive) and Attentiveness (e.g. perceptive, organised, helpful). Inter-rater reliabilities of ratings and internal consistencies of components were acceptable, and individual scores on each personality component predicted relevant behaviours within the Living Links (LL) capuchins up to a year later. For instance, individual scores on Sociability were positively related to the amount of time subjects spent in close proximity to others.

From a PCA of ten affiliative and agonistic behaviours, the social relationship structure (i.e. how many components and the characteristics of those components) of the LL capuchins was determined in Chapter 4. This chapter also assessed the effect of using three different methods of component extraction (Kaiser’s criterion, scree tests, parallel analysis) on the final PCA solution. Capuchins’ social relationships were best defined in terms of their “affiliative” and “agonistic” components, whereby higher scores on the affiliative component and lower scores on the agonistic component indicated overall “higher-quality” relationships.

In Chapter 5, an analysis comparing monkeys' scores on each relationship component with similarities in each dyadic partner's rank, age, sex, kinship, and personality revealed that similarity in Sociability was the sole predictor of affiliative relationship scores while age, rank, and Openness all had independent effects on agonistic relationship scores. These findings highlight the importance of personality homophily (i.e. affinity towards those individuals with similar personality traits; Massen and Koski 2014) in shaping the social relationships of capuchins, and more importantly, that personality homophily contributes to dyadic variation in the social relationship quality of these animals beyond what can be explained merely by basic social rules (i.e. kinship, age, sex, and rank).

Chapter 6 found that each monkey's mean relationship quality score (i.e. affiliative relationship scores minus agonistic relationship scores) with others in their group was significantly related to their position within their group's spatial proximity network, reflecting previous studies showing that capuchins that spend more time in close proximity engage in more affiliative rather than agonistic behaviour. Subjects' positions within their group's spatial network were positively related to rank, Sociability, and Assertiveness, but negatively related to Neuroticism; however, only rank and Sociability had independent effects on centrality. These latter findings agree with findings from Chapter 5, with Sociability and rank being the strongest predictors of the quality of subjects' affiliative and agonistic relationships, respectively. Collectively, these results illustrate the importance of individual differences in social network position, particularly beyond the explanatory power of basic social rules.

In Chapter 7, individual differences in learning were assessed among the LL capuchins under conditions of free-choice participation. For those subjects that frequently chose to participate on each task (>50% session participation), average task performance could not be explained by individual differences in age, attention span, scrounging behaviour, or time spent feeding within main enclosures. However, individual differences in Assertiveness were inversely related to performance, suggesting that these learning tasks were biased towards those individuals with lower Assertiveness; the other four personality traits (Openness, Neuroticism, Sociability and Attentiveness) were not significantly related to performance. Collectively, these findings illustrate that subjects' performances on these learning tasks may not necessarily be reflective of individual differences in their learning capacity *per se*, but rather individual differences in their willingness to apply their learning skills to solve tasks in general.

In Chapter 8, a negative relationship was found between the average learning performance of each subject and social success (i.e. spatial network centrality). Average learning performance was also negatively related to subjects' social rank and the number of affiliative acts subjects gave to other group members. Controlling for Assertiveness (which in Chapter 7 was the only factor related to monkeys' learning performance on both operant tasks), these relationships were no longer significant, suggesting that the relationship between learning and social success may be mediated through individual differences in rank-related personality.

A summary of the variables that were significantly related to subjects' social success (i.e. social rank and social network centrality) are illustrated in Figure 39. Further research using a larger sample of monkeys is necessary to test for underlying latent variables and error terms.

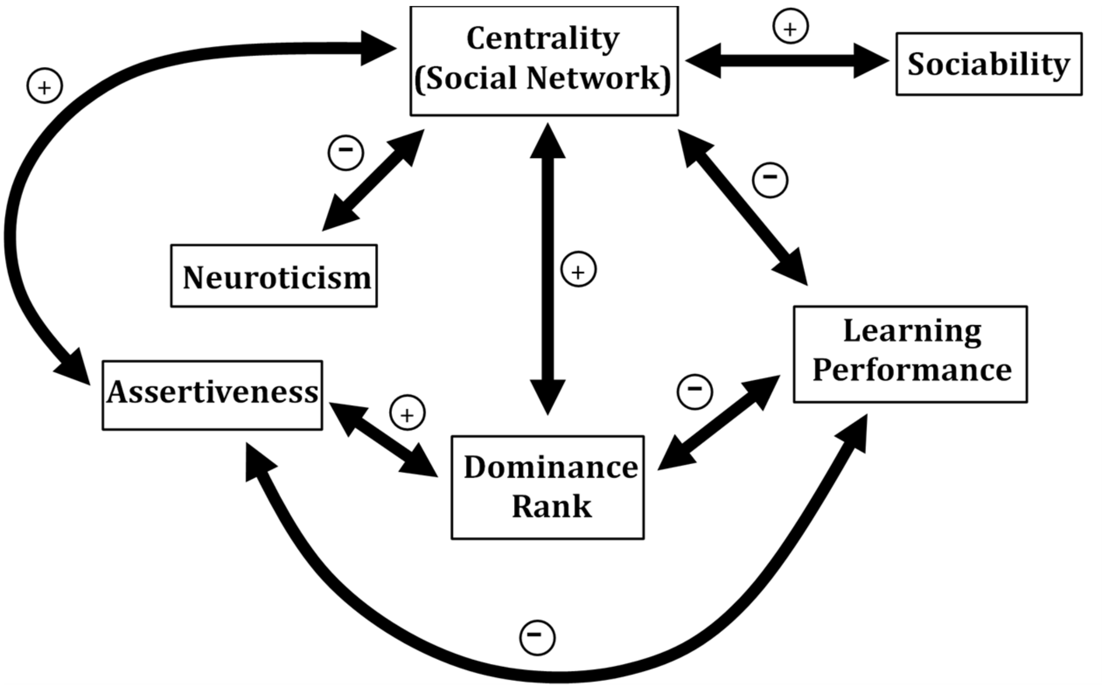


Figure 38. A summary of the variables that were significantly related to capuchins’ learning performance and social success, i.e. social network centrality; positive and negative symbols indicate the direction of each correlation.

Revisiting the hypotheses outlined in Chapter 1, the results of this thesis do not support the prediction that individual differences in learning performance are positively related to differences in social success. Rather, the findings are more supportive of hypotheses generated from studies of behavioural innovation and personality; that is, better learners should be lower ranking and less socially embedded than poorer learners. Moreover, in these capuchins, the relationship between learning and social success could be mediated through individual differences in personality (i.e. Assertiveness).

Pawlowski et al. (1998) reported that the relationship between male rank and mating success was negatively correlated with species differences in relative neocortex size. Dunbar (1998) later wrote that “this is just what we would predict if the lower ranking males of species with larger neocortices were able to use their greater computational capacities to deploy more sophisticated social skills, such as the use of coalitions and capitalizing on female mate choice, to understand or circumvent the power-based strategies of the dominant animals” (Dunbar 1998, p. 185). While the results of this thesis partly support this notion (i.e. better learners appeared to be more subordinate), there was no evidence to suggest that better-learning capuchins engaged in affiliative acts (including coalitions) more so than poorer learners, nor was there evidence that better learners targeted those individuals more socially successful than themselves. Rather, better learners were less likely to direct affiliative acts to other group members in general. As noted in Chapter 8, however, this result could reflect social “inflexibility”. In particular, it was suggested in Chapter 8 that better learners from prior studies on learning and social rank may have avoided using affiliative strategies to improve their social status due to the costs of status conflicts (e.g. physical aggression; Drea and Wallen 1999). Although brown capuchins are relatively tolerant of the close proximity of others, including non-kin, during feeding contexts, and also exhibit relatively low rates of agonism within their groups (Cooper et al. 2001; Fragaszy et al. 2004; Perry 2011), this thesis found similar results to those reported for macaques and ring-tailed lemurs (Strayer 1976; Bunnell et al. 1980; Bunnell and Perkins 1980; Kendal 2010*)*, which are often considered to have a less "tolerant" social organization compared to capuchins (Fragaszy et al. 2004). Negative relationships between learning and social success may therefore be generalizable across primate species living under social dominance hierarchies. Alternatively, if individual differences in personality underlie differences in learning performance (Chapter 7), an underlying biological mechanism may exist which mediates subjects' decision-making on tasks. Again, as discussed in Chapter 8, studies across numerous taxa, including non-primate species, have reported that individuals with more assertive personality traits have a tendency to make hasty decisions when solving tasks, resulting in poorer performance on tasks compared to individuals with less assertive personalities (Sih and Giudice 2012); such consistency in results across a wide range of phylogenetically distant taxa (e.g. fish, insects, mice, and primates) may be reflective of common underlying biological mechanisms.

Another possible explanation for the results of this study could be that individual capuchins lose motivation to learn as and when they obtain higher status, since applying one's learning skills to solve social challenges may no longer be necessary once higher status has been achieved. In rhesus macaques, Bunnell and Perkins (1980) noted that an increase in social rank resulted in a decrease in learning performance, suggesting that both variables were linked. Therefore, in terms of the SIH, better learners could still be using their skills to achieve higher status, but not in the conventional sense that socially successful individuals are *concurrently* better learners. As discussed in Chapter 1 and 8, there is a general tendency for researchers to imply that a positive correlation between intelligence and social success should exist among individual primates whereby more "intelligent" individuals ultimately achieve greater social success (e.g. Humphrey 1976; Sallet et al. 2011). Thus, if learning and social success are inversely related, there may be overlap between the SIH and what studies of behavioural innovation predict: that better learners are low-status individuals who use their skills to achieve social success, and over time those individuals loose the motivation (or need) to use those skills as and when higher-status is obtained. However, if poorer learners were indeed at some point better learners and used those skills to climb the "social ladder", as reflected by positive associations between relative brain size and rates of affiliative behaviour across species (e.g. Lehmann et al. 2007), then at the individual level there should also exist evidence whereby better learners are concurrently engaging in affiliative acts more than poorer learners since this may ultimately lead to their acquiring higher status at some point in the future. This, however, was not the case in the present study; there was a significantly *negative* correlation between learning performance and rates of affiliative behaviour among subjects, suggesting (for whatever reason) that better learners were not using affiliative strategies more so than poorer learners to acquire higher status within their groups. Further research is needed on capuchins' learning abilities during times of group instability (e.g. alpha take-over) to determine whether higher-status individuals (i.e. "poorer learners" during socially stable times) show improvements in their learning performance.

Collectively, none of the proposed scenarios underlying the results of this study are mutually exclusive *per se*, and further research is needed to examine each possibility in greater detail. Nevertheless, while the SIH works very well at the higher taxonomic level (see Chapters 1 and 8), as has been illustrated in this thesis, testing this hypothesis at the individual level is not clear-cut. Learning performance does not appear to have an independent relationship with the social success of individual primates, and factors like personality and social rank appear to be more important predictors of individual patterns of sociality and social success than is task performance. Further studies on primate personality and how it interacts with individual differences in social strategies and performance on learning and cognitive tasks will undoubtedly lead to a better understanding of the evolution of primate intelligence.

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Appendix

Table 1. Estimated relatedness in East group.

	Junon	Carlos	Chico	Kato	Manuel	Penny	Anita	Coeff. of Relatedness
Junon		0.5	0.5	0	0	0	0	0.166666667
Carlos	0.5		0.25	0	0	0	0	0.125
Chico	0.5	0.25		0	0	0	0	0.125
Kato	0	0	0		0	0	0	0
Manuel	0	0	0	0		0.25	0.5	0.125
Penny	0	0	0	0	0.25		0.5	0.125
Anita	0	0	0	0	0.5	0.5		0.166666667

Table 2. Estimated relatedness in West group.

	Lana	Figo	Toka	Pedra	Sylvie	Santi	Micoe	Inti	Coeff. of Relatedness
Lana		0.5	0.5	0.5	0.5	0.5	0.25	0.5	0.464285714
Figo	0.5		0.25	0.25	0.25	0.25	0.125	0.25	0.267857143
Toka	0.5	0.25		0.25	0.25	0.25	0.125	0.25	0.267857143
Pedra	0.5	0.25	0.25		0.25	0.25	0.125	0.25	0.267857143
Sylvie	0.5	0.25	0.25	0.25		0.25	0.125	0.25	0.267857143
Santi	0.5	0.25	0.25	0.25	0.25		0.125	0.25	0.267857143
Micoe	0.25	0.125	0.125	0.125	0.125	0.125		0.125	0.142857143
Inti	0.5	0.25	0.25	0.25	0.25	0.25	0.125		0.267857143

Table 3. Raw behavioural data for each monkey.

Monkey	**Age (Years)**	**% Time Feeding**	**% Time Moving**	**% Time Resting**	**% Time Playing**	**% Time Alert**	**% Time Being Groomed**	**% Time Grooming Others**	**Number of Times Aggressive**	**% Time Solitary**	**Average Attention Span Score**
Anita[a]	14	21.79	16.2	12.29	1.12	26.82	3.91	8.94	11	44.13	2.05
Carlos	5	45	15.56	7.78	12.22	10	0	0	0	78.89	2.53
Chico	2	18.89	8.33	20	24.44	10.56	4.44	0	2	48.89	2.27
Diablo[a]	40	31.38	18.09	4.79	0.53	35.64	2.66	2.13	11	55.32	
Diego	10	20.88	15.38	13.19	8.24	27.47	0	0	6	67.03	1.83
Figo	5	36.11	8.89	3.89	13.33	24.44	0.56	1.11	6	64.44	2.01
Inti	2	25.95	17.3	11.35	17.3	21.08	2.7	0	4	46.49	2.08
Junon	11	33.33	21.11	8.89	0	16.67	1.67	6.11	6	69.44	2.61
Kato	6	30.56	26.11	1.67	8.33	24.44	3.88	0	2	84.44	2.08
Lana[a]	11	20.9	17.51	5.65	0	25.99	3.95	9.6	10	28.81	
Manuel	4	32.04	23.76	3.87	1.66	30.94	0	1.1	2	73.48	2.11
Micoe	3	35.56	11.67	21.11	4.44	16.67	2.22	0	0	60	2.26
Pedra	3	31.11	15	1.11	12.78	31.67	0	0	3	76.67	2.27
Penelope	6	31.67	18.89	3.33	0.56	27.78	0.56	8.33	5	50	1.72
Popeye[a]	10	31.28	8.38	13.97	0.56	23.46	1.68	3.91	20	54.19	
Santi	9	20.67	8.94	16.2	0	21.79	0.56	18.44	3	41.9	2.83
Sylvie	8	34.44	10	7.22	0	25	2.78	10.56	4	48.33	2.44
Toka	7	30	18.89	1.11	0.56	42.22	0	0	3	96.11	

a=alpha status.

Table 4. Raw behavioural observations for each monkey dyad used to calculate social relationship structure using PCA.

Monkey Dyad	Food Sharing	Coalitions	Conflict	Grooming	Social Foraging	Spatial Proximity	Grooming Symmetry	Conflict Symmetry	Food Sharing Symmetry	Avoid/Stay Symmetry
Popeye-Anita	5	3	0	10	18	24	2	0	5	-31
Popeye-Junon	0	0	0	3	10	8	-3	0	0	-4
Popeye-Kato	0	0	1	5	0	0	5	1	0	
Popeye-Carlos	1	0	3	0	2	6	0	3	1	0
Popeye-Chico	0	0	7	1	2	6	1	7	0	-5
Popeye-Manuel	0	0	1	1	5	10	1	1	0	-5
Popeye-Penelope	1	1	2	4	18	41	0	2	1	-46
Anita-Junon	0	2	0	3	1	16	1	0	0	0
Anita-Kato	0	0	4	4	0	1	4	0	0	0
Anita-Carlos	0	0	3	3	0	1	3	3	0	0
Anita-Chico	0	0	5	3	2	19	3	5	0	-2
Anita-Manuel	2	1	0	0	4	16	0	0	-2	-5
Anita-Penelope	0	2	1	9	17	35	-1	1	0	-20
Junon-Kato	0	0	2	0	0	1	0	2	0	0
Junon-Carlos	0	0	1	0	2	0	0	1	0	-1
Junon-Chico	1	0	1	1	6	3	1	1	1	-31
Junon-Manuel	0	0	0	1	1	2	1	0	0	-2
Junon-Penelope	0	0	1	3	1	9	-3	-1	0	0
Kato-Carlos	0	0	0	0	0	0	0	0	0	0
Kato-Chico	0	0	0	0	0	12	0	0	0	-1
Kato-Manuel	0	0	1	0	0	6	0	-1	0	
Kato-Penelope	0	0	0	0	0	0	0	0	0	
Carlos-Chico	0	0	0	0	4	31	0	0	0	-10
Carlos-Manuel	0	0	0	2	6	13	-2	0	0	-2
Carlos-Penelope	0	0	1	1	1	1	-1	-1	0	0
Chico-Manuel	0	0	0	4	5	27	-4	0	0	-2
Chico-Penelope	0	0	3	1	5	23	-1	-3	0	-7
Manuel-Penelope	0	0	0	1	11	3	-1	0	0	-6
Diablo-Lana	1	0	0	10	11	28	4	0	1	-7

Diablo-Toka	0	0	1	0	0	0	0	1	0	
Diablo-Diego	0	0	0	0	3	6	0	0	0	-2
Diablo-Figo	1	0	5	0	7	9	0	5	1	-6
Diablo-Mekoe	0	0	1	0	13	4	0	1	0	-10
Diablo-Pedra	0	0	0	0	0	1	0	0	0	
Diablo-Santi	0	0	1	4	1	22	-2	1	0	-8
Diablo-Sylvie	1	0	0	1	9	24	-1	0	-1	-2
Diablo-Inti	1	2	0	0	15	14	0	0	1	-14
Lana-Toka	0	0	0	0	0	0	0	0	0	
Lana-Diego	0	0	0	0	3	10	0	0	0	-2
Lana-Figo	0	0	4	3	5	18	-1	4	0	-3
Lana-Mekoe	0	0	2	2	1	7	0	2	0	0
Lana-Pedra	0	0	0	0	0	7	0	0	0	0
Lana-Santi	3	2	0	22	22	86	-20	0	1	-6
Lana-Sylvie	0	0	0	11	16	41	2	0	0	
Lana-Inti	0	1	3	2	9	28	2	3	0	-5
Toka-Diego	1	0	0	0	3	0	0	0	-1	0
Toka-Figo	0	0	0	0	0	1	0	0	0	0
Toka-Mekoe	0	0	0	0	2	3	0	0	0	
Toka-Pedra	0	0	1	0	0	0	0	-1	0	-6
Toka-Santi	0	0	0	0	0	1	0	0	0	
Toka-Sylvie	1	0	2	0	0	0	0	-2	-1	
Toka-Inti	0	0	1	0	2	1	0	-1	0	
Diego-Figo	1	0	1	0	6	19	0	1	-1	-10
Diego-Mekoe	0	0	3	0	2	11	0	3	0	-22
Diego-Pedra	0	0	0	0	1	5	0	0	0	0
Diego-Santi	0	0	0	0	0	12	0	0	0	-4
Diego-Sylvie	1	0	0	2	2	5	2	0	-1	-3
Diego-Inti	0	0	2	1	8	20	1	2	0	-22
Figo-Mekoe	3	0	0	0	6	5	0	0	-1	-35
Figo-Pedra	2	0	0	0	7	14	0	0	-2	-12
Figo-Santi	0	0	4	0	2	0	0	0	0	-8
Figo-Sylvie	0	0	0	0	0	1	0	0	0	-1

Figo-Inti	0	0	3	0	15	15	0	-1	0	-34
Mekoe-Pedra	0	0	0	0	3	18	0	0	0	-2
Mekoe-Santi	0	0	1	1	2	11	-1	-1	0	-7
Mekoe-Sylvie	1	0	0	2	11	20	-2	0	-1	-5
Mekoe-Inti	1	0	0	0	11	31	0	0	-1	-25
Pedra-Santi	0	0	0	0	2	3	0	0	0	-1
Pedra-Sylvie	0	1	2	0	12	5	0	-2	0	0
Pedra-Inti	0	0	0	0	1	3	0	0	0	-6
Santi-Sylvie	0	0	0	8	2	22	8	0	0	-1
Santi-Inti	1	0	0	4	8	31	4	0	-1	-4
Sylvie-Inti	3	0	0	0	2	12	0	0	1	-1

Table 5. Number of agonistic interactions in West group over a four-month sampling period.

	Diablo	Figo	Inti	Toka	Lana	Sylvie	Pedra	Diego	Santi	Mekoe	TOTAL
Diablo		6	0	1	0	0	0	0	1	2	10
Figo	0		1	0	0	1	0	0	4	0	6
Inti	0	2		1	0	0	0	0	0	0	3
Toka	0	0	0		0	0	0	0	0	0	0
Lana	0	4	4	0		0	0	0	0	3	11
Sylvie	0	0	0	2	0		2	0	0	0	4
Pedra	0	0	0	3	0	0		0	0	0	3
Diego	0	1	2	0	0	0	0		0	3	6
Santi	0	2	0	0	0	2	0	3		1	8
Mekoe	0	0	0	0	0	0	0	0	0		0
TOTAL	0	15	7	7	0	3	2	3	5	9	51

Table 6. David's scores calculations for West group.

	Diablo	Figo	Inti	Toka	Lana	Sylvie	Pedra	Diego	Santi	Mekoe	W	w2	DS
Diablo		1	0	1	0	0	0	0	1	1	4	5.3333	9.3333
Figo	0		0.333	0	0	1	0	0	0.667	0	2	4.7778	-0.333
Inti	0	0.667		1	0	0	0	0	0	0	1.6667	1.3333	-1.667
Toka	0	0	0		0	0	0	0	0	0	0	0	-9.333
Lana	0	1	1	0		0	0	0	0	1	3	3.6667	6.6667
Sylvie	0	0	0	1	0		1	0	0	0	2	1	-4.667
Pedra	0	0	0	1	0	0		0	0	0	1	0	-2
Diego	0	1	1	0	0	0	0		0	1	3	3.6667	4
Santi	0	0.333	0	0	0	1	0	1		1	3.3333	5.6667	4.6667
Mekoe	0	0	0	0	0	0	0	0	0		0	0	-6.667
L	0	4	2.333	4	0	2	1	1	1.667	4			
l2	0	3.111	2.333	5.333	0	5.667	2	1.667	2.667	2.667			

Table 7. Number of agonistic interactions in East group over a four-month sampling period.

	Junon	Kato	Carlos	Anita	Chico	Penelope	Manuel	Popeye	TOTAL
Junon		2	3	0	1	0	0	0	6
Kato	0		0	2	0	0	0	0	2
Carlos	0	0		0	1	1	1	0	3
Anita	1	2	9		6	6	1	0	25
Chico	0	0	5	0		0	2	0	7
Penelope	2	0	5	0	8		3	1	19
Manuel	0	1	1	0	1	4		0	7
Popeye	0	1	4	0	9	12	3		29
TOTAL	3	6	27	2	26	23	10	1	98

Table 8. David's scores calculations for East group.

	Junon	Kato	Carlos	Anita	Chico	Penelope	Manuel	Popeye	W	w2	DS
Junon		1	1	0	1	0	0	0	3	2.833	0.6722
Kato	0		0	0.5	0	0	0	0	0.5	2.75	-6.172
Carlos	0	0		0	0.167	0.1667	0.5	0	0.8333	2.009	-12.67
Anita	1	0.5	1		1	1	1	0	5.5	11.33	14.577
Chico	0	0	0.8333	0		0	0.6667	0	1.5	2.298	-8
Penelope	1	0	0.8333	0	1		0.4286	0.07692	3.3388	6.604	3.7949
Manuel	0	1	0.5	0	0.333	0.5714		0	2.4048	3.325	-5.167
Popeye	0	1	1	0	1	0.9231	1		4.9231	13.82	18.462
L	2	3.5	5.1667	0.5	4.5	2.6612	3.5952	0.07692			
l2	3.1612	5.9222	10.342	1.75	7.298	3.4865	7.3008	0.20471			

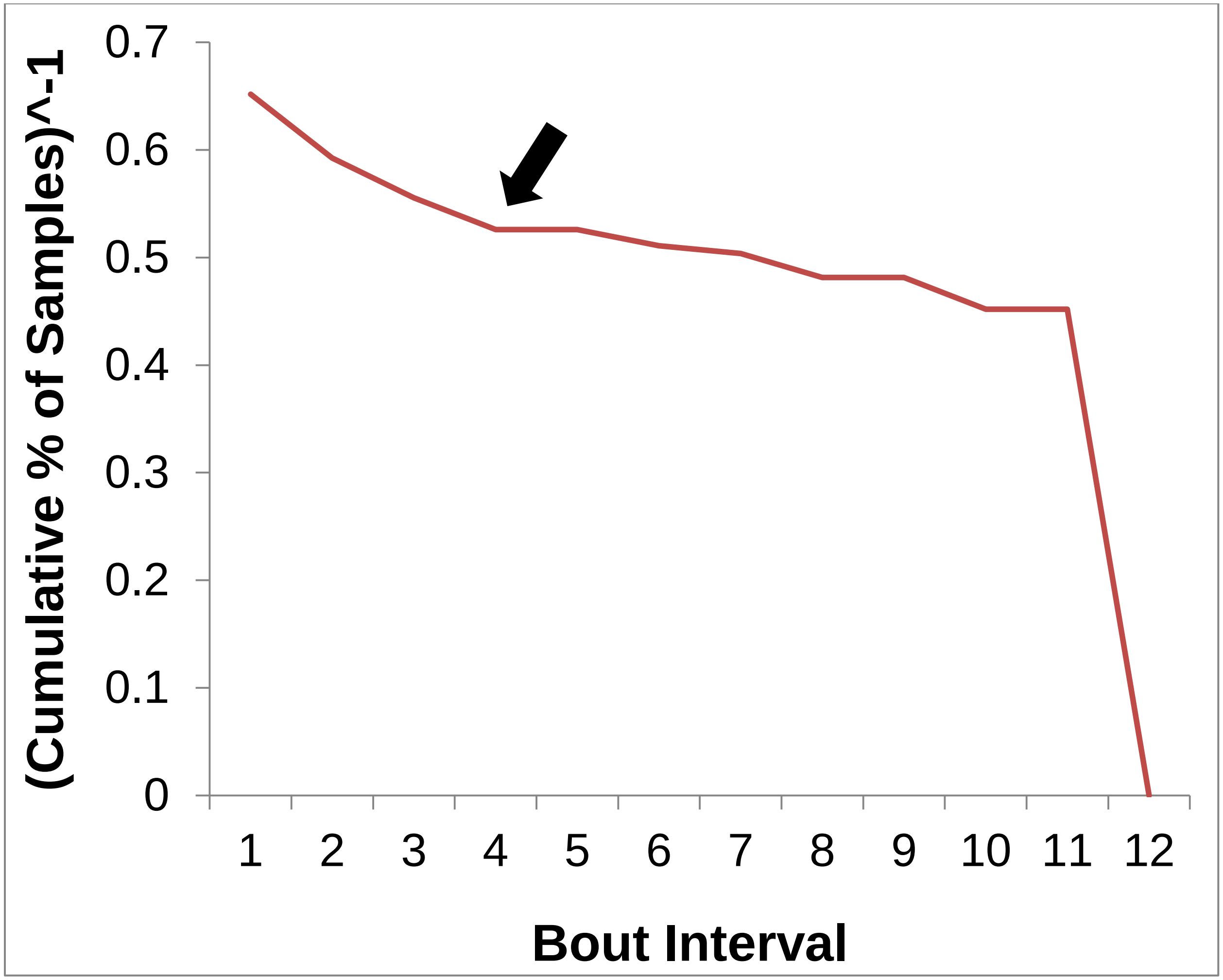

Figure X. Log survivorship curve for bout analysis. Black arrow indicates point at which intervals between grooming samples mark the start of a "new" bout of grooming. Slope after 10 seconds drops dramatically because sampling periods lasted only for 10 seconds.

Table 9. Inter-rater reliabilities for item ratings.

Adjective	***ICC*(3,1)**	***ICC*(3,*k*)**
Playful	0.75	0.91
Submissive	0.61	0.84
Aggressive	0.60	0.83
Vulnerable	0.58	0.82
Dominant	0.57	0.82
Bullying	0.56	0.81
Timid	0.55	0.81
Anxious	0.51	0.77
Active	0.50	0.77
Inventive	0.49	0.76
Innovative	0.46	0.74
Gentle	0.46	0.74
Solitary	0.45	0.73
Stingy/Greedy	0.45	0.73
Autistic	0.44	0.73
Inquisitive	0.44	0.73
Intelligent	0.42	0.71
Sociable	0.42	0.71
Defiant	0.41	0.70
Fearful	0.41	0.70
Lazy	0.41	0.70
Cautious	0.40	0.69
Imitative	0.39	0.68
Jealous	0.38	0.68
Dependent/Follower	0.38	0.67
Conventional	0.37	0.66
Impulsive	0.34	0.63
Irritable	0.33	0.62
Clumsy	0.33	0.62
Persistent	0.32	0.61
Curious	0.31	0.60
Distractible	0.31	0.60
Affectionate	0.30	0.59

Erratic	0.29	0.58
Excitable	0.29	0.57
Manipulative	0.28	0.57
Depressed	0.28	0.57
Protective	0.28	0.57
Reckless	0.28	0.56
Friendly	0.26	0.55
Disorganized	0.25	0.53
Sympathetic	0.23	0.50
Predictable	0.23	0.50
Thoughtless	0.22	0.49
Independent	0.22	0.49
Decisive	0.21	0.47
Helpful	0.19	0.45
Individualistic	0.19	0.45
Stable	0.19	0.44
Cool	0.17	0.41
Unemotional	0.17	0.40
Quitting	0.14	0.36
Sensitive	0.13	0.33
Unperceptive	0.12	0.32

Note. Estimates based on 121 capuchin monkeys, each rated by an average of 3.35 raters. *ICC*(3,1) = Reliability of individual ratings. *ICC*(3,*k*) = Reliability of a mean ratings.

Table 10. Six-component personality structure.

Item	**Varimax Rotated Components**						**Promax Rotated Components**					
	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC1**[a]	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**
Submissive	**-.92**	-.10	.01	-.15	-.18	.00	**-.93**	.07	-.04	-.18	-.17	.07
Bullying	**.91**	-.01	.06	-.18	-.06	.04	**.97**	-.16	-.01	-.15	-.04	.00
Aggressive	**.90**	.05	.07	-.19	-.08	.03	**.94**	-.09	.00	-.15	-.07	-.01
Stingy/Greedy	**.86**	.02	.04	-.17	.05	.21	**.90**	-.13	.02	-.16	.08	.18
Jealous	**.80**	.17	.03	-.21	.03	.26	**.80**	.04	.00	-.21	.06	.23
Gentle	**-.79**	-.11	-.15	**.40**	.11	.08	**-.85**	.01	-.02	.36	.09	.09
Dominant	**.79**	-.24	-.01	.06	.04	**.42**	**.85**	-.39	.04	.07	.10	.39
Vulnerable	**-.79**	-.07	.16	-.19	-.22	.04	**-.81**	.08	.11	-.19	-.18	.11
Timid	**-.71**	**-.44**	.10	-.28	-.21	-.05	**-.63**	-.34	.00	-.31	-.14	.02
Cautious	**-.71**	**-.46**	.05	-.14	-.13	.08	**-.64**	-.37	.01	-.18	-.05	.15
Manipulative	**.63**	**.42**	-.03	.02	.21	-.18	**.59**	.31	-.03	.03	.15	-.23
Fearful	**-.62**	-.32	.29	-.39	-.21	.00	**-.55**	-.23	.19	-.39	-.10	.09
Irritable	**.62**	-.05	.04	**-.41**	-.27	.15	**.67**	-.12	-.11	**-.40**	-.25	.15
Dependent/Follower	**-.61**	.12	.25	-.30	.28	-.24	**-.61**	.16	.23	-.33	.35	-.15
Independent	**.61**	.13	-.03	**.48**	-.28	.10	**.55**	.12	.06	**.59**	-.35	.00
Anxious	**-.55**	-.37	.26	-.34	**-.41**	-.01	**-.47**	-.26	.14	-.32	-.32	.06
Reckless	**.51**	**.47**	**.48**	-.13	.01	.21	**.43**	**.40**	**.53**	-.04	.09	.22
Autistic	**-.43**	-.24	.21	-.09	**-.42**	.05	**-.41**	-.12	.15	-.04	-.38	.08
Protective	**.42**	-.02	-.30	.23	.30	-.02	**.43**	-.12	-.24	.19	.24	-.08
Inventive	.12	**.86**	-.09	.12	.07	.22	-.09	**.90**	-.03	.12	-.03	.19
Inquisitive	.19	**.84**	.04	.05	.23	.18	.00	**.84**	.13	.06	.18	.17
Innovative	.07	**.84**	-.15	.08	.09	.20	-.14	**.89**	-.11	.06	-.02	.18
Playful	.08	**.83**	.11	-.09	.25	.02	-.09	**.83**	.15	-.09	.21	.03
Active	.05	**.81**	-.11	-.33	.24	-.08	-.09	**.82**	-.19	-.39	.15	-.07
Conventional	-.12	**-.79**	-.22	.17	.09	-.02	.04	**-.84**	-.19	.12	.13	-.02
Lazy	-.07	**-.71**	.32	.32	-.18	.06	.06	**-.72**	**.43**	**.42**	-.05	.06
Imitative	-.02	**.68**	-.05	-.04	.38	.03	-.16	**.67**	.00	-.08	.34	.04
Defiant	**.48**	**.59**	.25	-.07	-.13	.03	.37	**.58**	.24	.02	-.16	.01
Quitting	.00	**-.40**	.37	-.06	.01	-.31	.13	**-.46**	.37	.01	.11	-.29
Disorganized	-.22	.04	**.79**	-.07	-.26	-.08	-.22	.10	**.83**	.09	-.12	-.02
Unperceptive	.03	-.07	**.78**	-.10	-.08	-.01	.08	-.10	**.85**	.04	.11	.04
Thoughtless	-.12	.01	**.74**	-.15	-.16	.33	-.12	.02	**.82**	-.03	.05	**.41**

Distractible	.08	.01	**.70**	-.27	.31	-.25	.16	-.10	**.74**	-.20	**.49**	-.18
Clumsy	-.17	-.21	**.68**	.15	.06	-.15	-.11	-.23	**.81**	.28	.22	-.10
Erratic	.11	.30	**.61**	**-.41**	-.25	-.13	.10	.31	**.52**	-.30	-.16	-.08
Impulsive	.03	**.46**	**.50**	**-.49**	-.16	-.08	-.02	**.48**	**.40**	**-.42**	-.09	-.02
Helpful	-.22	.23	**-.45**	.34	.25	.14	-.32	.27	-.35	.26	.14	.10
Sensitive	-.29	-.06	-.38	.28	.29	.00	-.32	-.04	-.30	.20	.22	-.02
Intelligent	.09	.37	-.38	.29	.02	.03	-.02	**.41**	-.34	.27	-.12	-.03
Cool	.17	.04	-.30	**.78**	.14	.17	.09	.02	-.08	**.80**	.05	.08
Unemotional	.01	-.12	-.04	**.75**	.16	-.09	-.01	-.13	.19	**.81**	.13	-.16
Excitable	.00	.12	**.54**	**-.63**	-.03	-.07	.05	.09	**.42**	**-.60**	.11	.02
Predictable	-.08	**-.43**	-.05	**.60**	.05	.06	-.05	**-.43**	.13	**.64**	.06	.02
Sympathetic	-.35	.06	-.28	**.49**	.35	.02	**-.41**	.08	-.11	**.45**	.29	.00
Sociable	.21	.26	.05	.18	**.82**	.10	.17	.10	.26	.12	**.89**	.11
Solitary	-.39	-.33	.03	.02	**-.74**	-.16	-.35	-.16	-.10	.10	**-.79**	-.16
Affectionate	-.15	.14	-.02	.33	**.74**	.02	-.19	.05	.21	.27	**.78**	.03
Friendly	-.32	.22	-.24	.22	**.69**	.06	-.38	.18	-.08	.11	**.69**	.07
Depressed	**-.44**	-.35	.26	-.04	**-.65**	-.03	**-.40**	-.19	.18	.05	**-.62**	.00
Individualistic	-.07	.33	.29	.26	**-.43**	-.07	-.17	**.45**	.32	**.40**	**-.48**	-.10
Persistent	.27	.26	.03	-.07	-.01	**.82**	.17	.23	.12	-.09	.06	**.83**
Curious	.05	**.46**	.02	-.09	.19	**.73**	-.09	**.45**	.12	-.15	.25	**.76**
Decisive	.36	.08	-.32	.30	.07	**.62**	.28	.03	-.20	.26	.04	**.57**
Stable	-.02	-.13	-.24	**.42**	.16	**.59**	-.07	-.14	-.05	.38	.17	**.57**

Note. Salient loadings are in boldface. PC=principal component.; [a] Component was reflected.

Table 11. Promax correlations between components (six-component solution).

	PC1	**PC2**	**PC3**	**PC4**	**PC5**
PC2	-0.35	----	----	----	----
PC3	0.02	-0.05	----	----	----
PC4	-0.05	0.01	-0.45	----	----
PC5	-0.04	0.26	-0.38	0.25	----
PC6	-0.13	0.03	-0.17	0.18	-0.06

Table 12. Communalities for the five-component solution.

Item	**Communalities**
Fearful	.711
Dominant	.784
Persistent	.572
Cautious	.696
Stable	.528
Autistic	.474
Curious	.556
Thoughtless	.678
Stingy.Greedy	.780
Jealous	.738
Individualistic	.228
Reckless	.764
Sociable	.778
Distractible	.718
Timid	.812
Sympathetic	.566
Playful	.766
Solitary	.737
Vulnerable	.734
Innovative	.778
Active	.848

Helpful	.499
Bullying	.874
Aggressive	.858
Manipulative	.614
Gentle	.842
Affectionate	.678
Excitable	.665
Impulsive	.730
Inquisitive	.830
Submissive	.896
Cool	.725
Dependent.Follower	.661
Irritable	.624
Unperceptive	.635
Predictable	.546
Decisive	.647
Depressed	.786
Conventional	.685
Sensitive	.393
Defiant	.612
Intelligent	.333
Protective	.406
Quitting	.396
Inventive	.803
Clumsy	.564
Erratic	.710
Friendly	.698
Anxious	.781
Lazy	.745
Disorganized	.719
Unemotional	.499

Imitative	.617
Independent	.569

Table 13. Communalities for 3-component solution for social relationship structure.

Behavioural Calculation	**Communalities**
Avoid-stay symmetry	.586
Food share	.564
Coalitions	.625
Conflict	.815
Grooming	.733
Social foraging	.716
Spatial proximity	.820
Groom symmetry	.591
Conflict symmetry	.810
Food share symmetry	.472

Table 14. Communalities for 2-component solution for social relationship structure.

Behavioural Calculation	**Communalities**
Avoid-stay symmetry	0.293
Food share	0.438
Coalitions	0.595
Conflict	0.769
Grooming	0.602
Social foraging	0.716
Spatial proximity	0.658
Groom symmetry	0.321
Conflict symmetry	0.751
Food share symmetry	0.357

Table 15. Mean relationship quality scores and centrality for each monkey.

Monkey	**Mean Affiliative Score**	**Mean Agonistic Score**	**Mean Relationship Quality Score***	**Eigenvector Centrality**
Anita	5.28	4.72	0.58	0.46
Carlos	-2.86	0.99	-3.85	0.23
Chico	-0.37	5.21	-5.57	0.37
Diablo	1.01	1.2	-0.17	0.38
Diego	-3.2	-0.84	-2.35	0.29
Figo	-0.71	3.83	-4.57	0.24
Inti	2.61	0.48	2.14	0.37
Junon	-1.43	-0.75	-0.68	0.27
Kato	-4.46	0.32	-4.78	0.06
Lana	5.7	0.11	5.59	0.42
Manuel	-1.37	-3.63	2.26	0.37
Mekoe	-0.45	-0.7	0.26	0.32
Pedra	-4.2	-4.81	0.61	0.14
Penelope	2.61	-1.14	3.74	0.45
Popeye	5.42	7.66	-2.22	0.43
Santi	2.43	-3.7	6.12	0.39
Sylvie	-0.17	-5.09	4.92	0.34
Toka	-5.84	-3.86	-1.99	0.06

*Mean affiliative score minus mean agonistic score.

Table 16. Individual differences in capuchins' personality.

Monkey	**Assertiveness**	**Openness**	**Neuroticism**	**Sociability**	**Attentiveness**
Anita	4.84	3.57	3.61	5.41	5.08
Carlos	3.47	5.41	3.9	6.02	5.53
Chico	3.78	4.98	4.45	6	4.52
Diablo	4.86	3.09	3.14	5.17	5.61
Diego	3.01	3.1	3.94	3.57	5.47
Figo	4.14	5.09	3.98	5.52	4.93
Inti	3.5	4.9	4.2	6.29	4.62
Junon	4.1	4.6	3.62	5.62	5.45
Kato	3.53	5.45	5.39	3.33	4.42
Lana	5.18	3.66	3.83	5.21	5.04
Manuel	3.08	3.56	4.06	4.4	5.35
Micoe	3.78	4.85	3.83	6.11	5.06
Pedra	2.95	4.3	4.19	5.59	5.42
Penelope	3.45	3.65	4.72	5.49	4.96
Popeye	4.49	3.28	3.62	4.72	4.97
Santi	3.74	3.94	3.57	5.21	5.42
Sylvie	2.91	4.15	3.26	5.54	5.56
Toka	2.61	3.77	4.35	3.62	5.04