Individual differences in nonhuman primates: Personality and its relationship to social interactions, socio-emotional perception and well-being.

Vanessa Wilson

PhD Psychology of Individual Differences
The University of Edinburgh
2016

Declaration

I hereby declare that I am the author of this thesis and the work herein is my own, except where acknowledgements are made. Included publications are my own work, except where indicated throughout. This work has not been submitted for any other degree or professional qualification.

Acknowledgements

This research was funded in part by The McGlashan Trust, The Sidney Perry Foundation, The Sir Richard Stapley Educational Trust, The Great Britain Sasakawa Foundation and Japan Society for the Promotion of Science.

There are many people to whom the completion of this thesis owes its thanks. I would like to thank my supervisors, Alexander Weiss and Elizabeth Austin, for their support, encouragement and flexibility throughout. I would also like to take this chance to acknowledge my co-authors and collaborators, who helped to make so much of this work happen: Timothy Bates, Carmen Lefevre, Blake Morton, Annika Paukner, Sarah Brosnan, Hannah Buchanan Smith, Rick D'Eath, Anthony Little, Marieke Gartner, Alaa El Shawaari, Miho Inoue-Murayama, Katie Slocombe, Emma Wallace and Drew Altschul. Stephanie Koksic, Emma Zaharieva, Molly Feldman and Leveda Cheng also deserve a big thank you for their assistance with data entry and video coding.

I am most grateful to my office mates and fellow Journal club members for their constructive criticism, advice, good humour and plentiful cake: Marieke Gartner, Mark Adams, Drew Altschul, Lauren Robinson, Milan Valášek, David Hill, Sebastian Sandoval Similä, Catherine Crompton, Stuart Richie, Iva Čukić, Nina Wirtz, Louisa Miller, Yolanda Zhao, Irina Kozlova, Linnea Lyckberg, Jia Loy, Yu mei Li, Conor Smith and Chloe Wright.

My appreciation also goes to all the zoos, keepers, research staff, chimpanzees and monkeys who took part in data collection, but especial thanks to the staff at Edinburgh Zoo whose time, patience and good humor has been vital to the majority of this research.

Lastly, I am indebted to the support of my family and friends throughout this PhD. In particular I would like to acknowledge Alina for all her encouragement; Charlotte for her wonderful DIY skills and assistance with equipment design; my parents Valerie and Chris, for their unending support, my grandparents Marjory, Reginald, John and Beryl, as well as Eilidh, Alfie, Wicket, Inka and Pepper, for their companionship, which has meant so much. Finally, I thank Milan, for getting me through to the end.

This thesis builds on the work of many, to whom I am ever grateful for their contributions to this subject. I hope that this field will continue to expand and be the subject of much further research, in line with the mission of the RZSS (1913) – *"To promote, facilitate and encourage the study of zoology and kindred subjects and to foster and develop amongst the people with an interest in and knowledge of animal life."*

This thesis is dedicated to the memories of Reginald Wilson and John (Enoch) Lavender, whose influence will go beyond their years.

Abstract

In recent years there have been efforts to assess associations between personality, longevity and well-being in nonhuman primates. Currently, findings indicate that, as in humans, personality traits such as extraversion are associated with both higher well-being (in monkeys and apes) and longevity (in gorillas). Why certain traits seem to have a protective effect is not yet well understood. One hypothesis is that more extraverted individuals rely on the company of others to alleviate stress, and thus mediate physiological stressors, increasing potential life span. Individual differences in social behaviour are therefore an important consideration for increasing our understanding of the protective effects of personality traits. The role of personality in social interactions and well-being is the main focus of this thesis. In Chapter 2, I assess personality and well-being in two species of New World monkey - common (*Saimiri sciureus*) and Bolivian squirrel monkeys (*Saimiri boliviensis*) - for which these associations have not previously been studied. I assess differences in personality trait structure between the two species, and compare them to a close relative, *Sapajus apella* (brown capuchins). I also correlate personality with well-being. Results show that both squirrel monkey species are similar in personality structure, but Bolivian squirrel monkeys share more similar traits with brown capuchins than common squirrel monkeys do. Well-being is associated with low Neuroticism and high Openness. These comparisons inform our understanding of the phylogeny of personality traits, as well as the ancestral links between personality and well-being. In Chapter 3 I focus on examining individual differences in chimpanzee (*Pan troglodytes)* traits, through the use of previously collected personality data, which may reflect something akin to autism in nonhuman primates. In Chapter 4

I examine behavioural correlates of these traits, and assess personality in relation to behaviour. Results indicate that personality is a stronger predictor of individual differences in social behaviour than the scale measuring autism-like traits. Continuing with a focus in chimpanzees, in Chapter 5 I examine whether personality predicts how individual chimpanzees perceive emotion in conspecifics, using both behavioural and experimental data. Findings show that individuals differ in their attention and arousal in response to emotions in others, and that personality plays a role in these responses. I also report different 'levels' of response indicative of separate arousal and attention based processes. This is an understudied but important area of research that might help to elucidate differences in coping with stressful situations in a group environment. In Chapter 6 I shift from a focus of personality as a predictor of response, to potential signals of personality, by examining personality correlates of facial morphology in brown capuchins, *Sapajus apella*. Results indicate that face width is associated with higher Assertiveness, whilst lower face height is associated with higher Neuroticism/lower Attentiveness. To assess the theory that these associations may act as social cues, such as signals of status or mate quality, in Chapter 7 I assess whether capuchins perceive differences in face width of conspecifics by measuring response to facial images. Results suggest that capuchins do not differ between wide and narrow faces. I discuss the possibility that perception of these associations may be dependent on other variables such as age or knowledge of the signal receiver. Overall, this thesis takes a broad approach to understanding personality, by examining its role in social interactions, perception of others and well-being. These findings are discussed in light of both evolutionary theory and potential benefits to welfare.

Note on publications and permissions

Some of the content of this thesis has been or will be published in peer-reviewed journals. These are detailed below, and relevant publications are included in Appendix D. In places throughout this thesis the term ‘we’ is used to acknowledge the input of collaborators and co-authors on this work.

Chapter 2: The personality data is under revision for publication:

Wilson, V., Inoue-Murayama, M. and Weiss, A. (under revision). A Comparison of Common and Bolivian Squirrel Monkey Personality.

Chapter 3: The contents have been published as a chapter in ‘Organism models of autism spectrum disorders’. Permissions are provided in Chapter 3.

Chapter 4: The contents of this chapter are in preparation for submission to a peer-reviewed journal. I acknowledge my collaborators Katie Slocombe and Emma Wallace for collecting and providing the behavioural data, and my supervisor Alex Weiss for providing the personality data.

Chapter 6: The contents have been published in *Personality and Individual Differences*. Permissions are provided in Chapter 6.

Chapter 7: The contents of this chapter are not published, but I acknowledge the contributions of my collaborators on this project: Alaa El Shawaari and Marieke Gartner helped with data collection; Hannah Buchanan Smith, Rick D’Eath and Blake Morton provided guidance and supervision; and Anthony Little provided manipulated images for the experimental set up.

I refer to four other publications in this thesis, one that is in press, and the other three which have been published in *PLoS ONE*, Behavioural Processes and Applied Animal Behaviour Science. All three papers are included in Appendix D.

Table of Contents

LIST OF TABLES 10

LIST OF FIGURES.. 15

CHAPTER 1. THE INTEGRATION OF PERSONALITY AND SOCIO-EMOTIONAL RESEARCH.. 18

1.1 INDIVIDUAL DIFFERENCES: THE CONCEPT OF PERSONALITY 18
1.1.1 The definition and measure of personality. 18
1.1.2 Why personality? 21
1.2 THE ROLE OF PERSONALITY IN FITNESS 27
1.2.1 Personality in health and well-being. 27
1.2.2 The genetics of personality 32
1.2.3 Morphological correlates of personality. 39
1.3 THE INTEGRATION OF PERSONALITY INTO A BROADER RESEARCH FRAMEWORK 44
1.4 EMOTIONAL PERCEPTION 45
1.4.1 The definition of emotional perception. 45
1.4.2 Taking a differential approach to emotional perception. 57
1.5 LINKING PERSONALITY TO EMOTIONAL AND SOCIAL PERCEPTION, SOCIAL INTERACTIONS AND WELL-BEING 59

CHAPTER 2. PERSONALITY AND WELL-BEING IN TWO SPECIES OF SQUIRREL MONKEY 62

2.1 THE DIVERSITY AND ORIGINS OF PERSONALITY 62
2.2 COMPARATIVE ASSESSMENT IN SQUIRREL MONKEYS 68
2.3 PERSONALITY AND WELL-BEING 71
2.4 METHODS FOR PERSONALITY ASSESSMENT 73
2.4.1 Subjects. 73
2.4.2 Instrument. 74
2.4.3 Analyses. 76
2.5 METHODS FOR WELL-BEING ASSESSMENT 78
2.5.1 Subjects. 78
2.5.2 Instrument. 79
2.5.3 Item reliabilities. 80
2.5.4 Well-being structure and relation to personality. 80
2.6 RESULTS FOR PERSONALITY ASSESSMENT 81
2.6.1 Species-level analyses 81
2.6.2 Cross-species comparisons. 90
2.7 RESULTS FOR WELL-BEING ASSESSMENT 103
2.7.1 Interrater reliabilities. 103
2.7.2 Well-being structure. 103
2.7.3 Well-being correlations with personality. 105
2.8 DISCUSSION OF PERSONALITY IN SQUIRREL MONKEYS 106
2.9 DISCUSSION OF WELL-BEING IN RELATION TO PERSONALITY 110
2.9.1 The role of well-being measures in welfare management. 111
2.10 FUTURE DIRECTIONS 112

CHAPTER 3. USING PERSONALITY TO MODEL BEHAVIOURAL EXTREMES.... 114

3.1 CHIMPANZEES AS A FOCUS SPECIES 114
3.2 THE COMPARATIVE APPROACH 116
3.3 USING PERSONALITY ASSESSMENT TO UNDERSTAND BEHAVIOURAL EXTREMES 117
3.4 SUMMARY 148

CHAPTER 4. PERSONALITY, AUTISTIC-LIKE TRAITS, STEREOTYPY AND SOCIAL INTERACTIONS IN CAPTIVE CHIMPANZEES 152

4.1 PERSONALITY, WELL-BEING AND WELFARE 152
4.2 METHODS 158
4.2.1 Subjects. *158*
4.2.2 Personality ratings and autism scores. *158*
4.2.3 Behaviours. *159*
4.3 RESULTS 166
4.3.1 Stereotypic behaviours. *166*
4.3.2 Social behaviours. *168*
4.4 DISCUSSION 169
CHAPTER 5. INDIVIDUAL DIFFERENCES IN EMOTIONAL PERCEPTION IN CHIMPANZEES 182
5.1 FROM SOCIAL INTERACTIONS TO EMOTIONAL PERCEPTION 182
5.2 ASSESSING EMOTIONAL PERCEPTION IN CHIMPANZEES 184
5.3 PART 1: BEHAVIOURAL OBSERVATIONS 185
5.4 METHODS 188
5.4.1 Subjects. *188*
5.4.2. Behavioural data. *188*
5.4.3 Video coding. *191*
5.4.4 Personality data. *192*
5.4.5 Analyses. *193*
5.5 RESULTS 208
5.5.1 Proportion response. *208*
5.5.2 Response behaviours. *208*
5.6 DISCUSSION 220
5.7 PART 2: EXPERIMENTAL 225
5.8 METHODS 229
5.8.1 Participants. *229*
5.8.2 Ethics. *229*
5.8.3 Stimuli. *229*
5.8.4 Set-up. *230*
5.8.5 Procedure. *232*
5.8.6 Coding. *234*
5.8.7 Analyses. *235*
5.9 RESULTS 236
5.9.1 Inter-coder reliability. *237*
5.9.2 Blank screen vs. video. *237*
5.9.3 Looking time to loops. *237*
5.9.4 Looking time to outcomes. *238*
5.9.5 Personality and looking time. *238*
5.10 DISCUSSION 240
5.11 PART 3: EXAMINING 'LEVELS' OF PERCEPTION 243
5.12 METHODS 246
5.12.1 Analyses. *246*
5.13 RESULTS 247
5.14 DISCUSSION 248
5.15 OVERALL DISCUSSION: BRINGING TOGETHER THE FINDINGS 250
CHAPTER 6. PERSONALITY AND FACIAL MORPHOLOGY IN BROWN CAPUCHINS 256
6.1 WHAT'S IN A FACE? 256
6.2 PERSONALITY MEASURES IN THE FACE 269
CHAPTER 7. IS THE CAPUCHIN FACE A CUE TO PERSONALITY? 272
7.1 PERSONALITY IN THE FACE: SIGNALS OR CUES? 272

7.2 DESIGNING A METHOD TO TEST RESPONSE TO FACIAL MORPHOLOGY 275
7.3 METHODS 281
    7.3.1 Sample. *281*
    7.3.2 Model design. *282*
    7.3.3 Procedure. *285*
    7.3.4 Analyses. *288*
7.4 RESULTS 289
    7.4.1 Training. *289*
    7.4.2 Interrater reliability. *289*
    7.4.3 Latency to approach. *289*
7.5 DISCUSSION 291
    7.5.1 Interpretation of results. *291*
    7.5.2 Limitations. *295*
    7.5.3 Summary and Future Directions. *296*

CHAPTER 8. PAYING ATTENTION TO INDIVIDUAL DIFFERENCES 300
8.1 SUMMARY 301
    8.1.1 The phylogeny of personality in relation to social structure. *301*
    8.1.2 Personality predicts atypical behaviour and social response. *303*
    8.1.3 Traits as social signals. *307*
8.2 CRITICAL EVALUATION 309
8.3 FUTURE DIRECTIONS 311

REFERENCES 314

APPENDIX A. SUPPLEMENTARY TABLES FROM CHAPTER 2 345

APPENDIX B. QUESTIONNAIRES USED IN DATA COLLECTION 348

APPENDIX C. SUPPLEMENTARY TABLES FROM CHAPTER 5 363

APPENDIX D. PUBLICATIONS 367

List of Tables

Table 1.1 Personality dimensions and facets in the human Five Factor Model……………………………………………………….. 20

Table 1.2 Developmental stages of Theory of Mind in humans and chimpanzees…..……………………………………………….…. 48

Table 1.3 The five levels of emotional perception………………………. 53

Table 2.1 Personality dimensions across species, determined using variants of the Hominoid Personality Questionnaire…………………… 64

Table 2.2 Descriptive statistics for information collected from each zoo... 75

Table 2.3 Item loadings on component structures for common squirrel monkeys……………………………………………………….. 82

Table 2.4 Item loadings on component structures for Bolivian squirrel monkeys……………………………………………………….. 86

Table 2.5 Age and sex effects on personality in common and Bolivian squirrel monkeys……………………………………………. 89

Table 2.6 Correlation coefficients between species personality-structure scores for squirrel monkeys and brown capuchins………….... 93

Table 2.7 Procrustes rotation: Solution matrix (Bolivians) is rotated onto the target matrix (commons)……………………………………… 95

Table 2.8 Item loadings on component structure for genus-level analysis of *Saimiri*…………………………………………………… 97

Table 2.9 Procrustes rotation: Solution matrix (commons) is rotated onto the *Saimiri* structure………………………………………………. 99

Table 2.10 Procrustes rotation: Solution matrix (Bolivians) is rotated onto the *Saimiri* structure……………………….....……………… 101

Table 2.11 Mean genus-level component *z*-scores for common and Bolivian squirrel monkeys…………………………………………….. 102

Table 2.12 Mean genus-level component *z*-scores by sex for common and Bolivian squirrel monkeys…………………………………… 103

Table 2.13 Genus-level personality components with species and sex effects……………………………………………………...… 104

Table 2.14 Correlation coefficients and bootstrapped confidence intervals for personality and well-being components in common and Bolivian squirrel monkeys…………………….....……...……105

Table 3.1 Factor structure from King & Figueredo (1997) for items derived from human personality assessment for use in chimpanzee assessment…………………….....…...………… 118

Table 1 (C. 3) Behavioural deficits and response to trauma as detailed in three species of apes…………………………………….……137

Table 2 (C. 3) Expected trait deficits in chimpanzees that would demonstrate neurodevelopmental deficits………………..….. 140

Table 3 (C. 3) Sex differences in the Autism Scale for the whole sample; number of males and females in the upper and lower quartiles of the scale………………………………………… 140

Table 4 (C. 3) Findings of predicted trait differences on the Autism Scale…………………………………………………...…….. 144

Table 5 (C. 3) Trait loadings defined as the difference between trait means of upper and lower quartiles on the Autism Scale…... 145

Table 4.1 Ethogram of behaviours recorded during individual focal observations……………………………………………… 162

Table 4.2 Ethogram for observations of all occurrence social grooming... 162

Table 4.3 Item loadings for each chimpanzee personality component.... 163

Table 4.4 Autism scores and personality components as predictors of regurgitation instances in the full sample.............................. 167

Table 4.5 Autism scores and personality components as predictors of regurgitation instances in the mean model…………………...167

Table 4.6 Effects of autism score and personality on nearest neighbour distance……………………………...…………………… 168

Table 4.7 Autism scores and personality on duration of grooming bouts for actor and recipient…………………………….………. 170

Table 4.8 Effects of autism scores and personality on social grooming vs. self grooming……………………………………….…. 171

Table 4.9 Effects of autism scores and personality on giving grooming vs. receiving grooming………………………………………. 171

Table 5.1 Sex and date of birth for all 18 adult chimpanzees that were observed…………………………………………………... 190

Table 5.2 Ethogram of emotional events and behavioural responses to emotional events, as well as sympathetic behaviours……….. 197

Table 5.3 Personality, age and sex as predictors of mean proportion response to all events in a linear model……………………... 208

Table 5.4 Personality components as predictors of mean proportion response to each event type, for all events…………………………… 209

Table 5.5 Personality, age and sex as predictors of mean proportion response to each event type………………………………… 209

Table 5.6 Frequency of response behaviours to all events and each event type……………………………………………………….. 210

Table 5.7 Principal components analysis of response behaviours using promax (top) and varimax (bottom) rotation………………... 211

Table 5.8 Component correlations determined by principal components analysis using promax rotation……………………………… 211

Table 5.9 Personality, age and sex as predictors of Move behaviour, separated into response to all events, and Displays Conflict and Hoots only…………………………………………….... 213

Table 5.10 Personality, age and sex as predictors of Look behaviour, separated into response to all events, and Display, Conflict and Hoots only…………………………………………………… 215

Table 5.11 Personality, age and sex as predictors of Interact behaviour, separated into response to all events, and Display, Conflict and Hoots only…………………………………………………… 216

Table 5.12 Personality, age and sex as predictors of Arousal behaviour, separated into response to all events, and Display, Conflict and Hoots only…………………………………………………… 218

Table 5.13 Personality, age and sex (top) and Neuroticism x outcome interaction (bottom) as predictors of proportion looking time to scenario outcomes…………………………………………... 238

Table 1 (C. 6) Means (and standard deviations) for personality dimensions and facial metrics…………………………….... 263

Table 2 (C. 6) Table of zero-order correlations among all personality and face variables…………………………………………… 264

Table 3 (C. 6) Regression of fWHR and face width/lower face height on demographic variables and personality……..…… 264

Table 7.1 Latency to approach models vs. monkey conditions and with additional predictors of age and sex ……………………….. 289

Table 7.2 Latency to approach predicted by contrast for all participants and for adults only………………...………….. 290

Table A1 ICCs for personality items in Bolivian and common squirrel monkeys and genus-level *Saimiri*……………………….…. 344

Table A2 Item loadings on well-being component for Bolivian squirrel monkeys……………………………………………........ 345

Table A3 Component structure from Morton Lee, Buchanan-Smith, et al., (2013) for personality items assessed in brown capuchins, *Sapajus apella* ……………………………………………………… 346

Table C1 Event descriptions and categories from behavioural observations……………………………………………….. 362

Table C2 Dates and times of behavioural observations for all chimpanzees……………………………………………….. 364

List of Figures

Figure 2.1 Common and Bolivian squirrel monkeys…………………… 70

Figure 3.1 Chimpanzees show many behavioural and cognitive parallels to humans…………………………………………………… 115

Figure 1 (C. 3) Origins of stereotypy in primates…………………… 136

Figure 5.1 The set up for the experimental study, for the indoor research room (left) and outdoor research room (right)……………… 230

Figure 5.2 Description of social scenarios…………………………….. .232

Figure 5.3 Association of Neuroticism with proportion looking time to the emotional and unemotional scenario outcomes….…….. 239

Figure 6.1 The faces of brown capuchins, *Sapajus apella*, are important in social communication…………………………..…….. 259

Figure 1 (C. 6) Measures and measuring points used for morphometric calculations……………………………………………….. 263

Figure 2 (C. 6) Linear fits of age against face width/lower face height, separately for each sex……………………………………… 264

Figure 3 (C. 6) Regression plot of lower face/face height against Neuroticism……………………………………………….. 265

Figure 4 (C. 6) Structural equation model predicting Assertiveness, Attentiveness to others and Neuroticism from fWHR and lower face/face height…………………………………………... 265

Figure 7.1 Images used for averted gaze conditions…………………… 276

Figure 7.2 Experimental set up at Living Links……………………….. 276

Figure 7.3 Average response latencies to each condition in each sample for (a) Living Links and (b) LRC………………..………….. 278

Figure 7.4 Stages of model design……………………………………… 283

Figure 7.5 In the wild capuchins often occupy dense foliage, meaning that parts of the body can be partially concealed from view…………………………………………………… 284

Figure 7.6 Experimental set up……………………………………….… 285

Figure 7.7 Latency to approach in the five different conditions for the full sample (n=14: top plot) and for adults only (n=8: bottom plot)………………………………………….. .291

Chapter 1. The Integration of Personality and Socio-emotional Research

> *"In my present thinking there is no question about the reality of chimpanzee mind, individuality, personality…. I ask only that you acquaint yourself with the essential features of anthropoid behaviour before pronouncing my assumption unpragmatic or illogical."*
>
> - Robert M. Yerkes (1939, p. 97)

1.1 Individual Differences: The Concept of Personality

1.1.1 The definition and measure of personality.

The concept of intra-specific differences began to come to light with Darwin, who observed the variability of traits that occurred within a species. He referred to them as individual differences, and noted the importance of such variation under the process of natural selection (Darwin, 1872). Yet the study of personality only began to develop in earnest from the 1920s, with Allport's focus on the descriptive trait approach; this work followed the concept of scoring used in IQ tests, except it did so with the collation of adjectives that could be used as personality trait descriptors (Allport & Odbert, 1936; Barenbaum & Winter, 2008). This work was soon followed by that of Catell and Eysenck, who were among the first to use a factor analytic approach to determine the covariance of personality adjectives (Barenbaum & Winter, 2008; Catell, 1945; Eysenck, 1977). This approach has been maintained in current day assessments of personality, and involves the grouping of items into factors or components which represent groups of correlated traits.

The idea behind this is that personality is made up of multiple, separate dimensions, but each of these dimensions plays a role in our behaviour; as defined by McCrae and John (1992), personality describes how individuals vary in emotions, attitudes and motivations. In humans there has been much effort to produce a single model of personality that is representative of human traits, and is replicable across samples (Digman, 1990). The currently accepted structure consists of five factors of personality, a result reached separately by both the Five Factor Model (FFM) and the Big Five (Goldberg, 1990; McCrae & Costa, 1987). Goldberg (1990) focused on a purely lexical approach, assessing personality using single trait adjectives. McCrae and Costa (1987) took an alternative approach with the NEO Personality Inventory, which used behavioural descriptions to assess personality. Both approaches agreed on the finding of five general trait groupings, although they differed in their factor labels: Whilst the FFM consists of Openness, Conscientiousness, Extraversion, Agreeableness and Neuroticism, the Big Five refers to these as Intellect, Conscientiousness, Surgency, Agreeableness and Emotional Stability; notably, the item loadings on this last factor are inverse to those found on Neuroticism. An additional difference between the two approaches is that, whilst the FFM divides each component into six facets of personality (see Table 1.1), the Big Five divides its components into a total of 75 scales with descriptors, for example, one scale is described as *Spirit: Jolly, merry, witty, lively, peppy* (Goldberg, 1990).

Table 1.1

Personality dimensions and facets in the human Five Factor Model

Factor	Facet
Extraversion	Warmth, Gregariousness, Assertiveness, Activity, Excitement Seeking, Positive Emotions
Agreeableness	Trust, Straightforwardness, Altruism, Compliance, Modesty, Tender-Mindedness
Conscientiousness	Competence, Order, Dutifulness, Achievement Striving, Self-Discipline, Deliberation
Neuroticism	Anxiety, Hostility, Depression, Self-Consciousness, Impulsiveness, Vulnerability
Openness	Fantasy, Aesthetics, Feelings, Actions, Ideas, Values

Note. Dimensions from Costa, McCrae, and Dye (1991).

Agreement on which labels to use to represent each dimension is wrought with debate – a label should be neither too broad, nor too narrow to describe the traits it encompasses. In current research, the original FFM labels have taken preference in describing these five factors (John, Naumann, & Soto, 2008). Items loading on Openness include conventional, creative and curious; Conscientiousness is described by item loadings such as careful, reliable and organised; Extraversion includes item loadings of sociable, affectionate and spontaneous; Agreeableness includes good-natured, sympathetic and forgiving; and Neuroticism is described by item loadings such as worrying, nervous and emotional (McCrae & Costa, 1987).

This structure has been repeatedly validated in the human population and become the primary model for use in human personality assessment (John et al., 2008).

In contrast, personality assessment in other species is still relatively in its infancy. Despite the fact that personality was recognised in nonhuman primates around the same time that Allport's work began in earnest (Crawford, 1938; Yerkes, 1939), only in the last decade has this field truly begun to expand. In the 2000s, there were almost 100 studies published on primate personality alone, which comprises almost half of the 210 primate studies conducted between the 1930s and 2000s (Freeman & Gosling, 2010). In this expanding field, it is becoming clear that personality is an important predictor of fitness, that is, the propensity of an organism to survive and reproduce[1] (Mills & Beatty, 1979; Sober, 2000); personality is implicated in coping with every day stressors, as well as long term survival. In the following section I address personality assessment in nonhuman animals (from here on referred to as animals), and why it is becoming an increasingly important consideration in behavioural research.

1.1.2 Why personality?

Why study personality? This is a recurrent question I have encountered from both primatologists and lay people. In considering an answer to this question, one must consider what personality means across contexts. For humans, it affects our political values, who we choose as social partners and mates, and how committed we are to our choices (Erdheim, Wang, & Zickar, 2006; McCrae & Sutin, 2009). Personality is also a predictor of health and mortality risk (Deary, Weiss, & Batty,

---

[1] But this is debated amongst evolutionary psychologists. How far should fitness extend – to offspring? Grandoffspring? If so then how do we measure it?

2010; Shipley, Weiss, Der, Taylor, & Deary, 2007), and is related to well-being (DeNeve & Cooper, 1998; Steel, Schmidt, & Shultz, 2008). In short, personality influences how we approach, and succeed, at life. It plays a crucial role in survival.

Given these findings, it is important to address whether similar associations exist in other species. People who work closely with animals, or who keep them as companions, can recognise and accurately rate individuals on personality descriptors (Freeman & Gosling, 2010; Gartner, 2015). These ratings tend to show interrater reliability, internal consistency and test-retest reliability (Freeman & Gosling, 2010), indicating that animal personality can be rated just as human personality can. In fact, a review of 12 studies that assessed primate personality in eight species, reported dimension-level interrater reliabilities of between 0.15 and 0.94, with an average of 0.75 (Freeman & Gosling, 2010). This is higher than interrater reliabilities reported in human research, which at the component level are no higher than 0.50 when people are rated by friends, family and acquaintances (Funder, Kolar, & Blackman, 1995). Internal consistencies are also high for animal ratings, with a mean alpha of 0.87 across 12 primate studies; furthermore, test-retest reliability, although reported in only five studies, ranged between 0.02 for Friendliness to humans and 0.98 for dimensions of Dominance and Physical Activity, with a mean of 0.66 (Freeman & Gosling, 2010).

Personality ratings have also been validated using behavioural observations (Capitanio, 1999; Konečná et al., 2008; Morton, Lee, Buchanan-Smith, et al., 2013; Pederson, King, & Landau, 2005). For example, in brown capuchins, subjects rated as high on Openness are observed to spend more time playing with others, and those with higher Sociability ratings spend more time within social cliques (Morton, Lee, Buchanan-Smith, et al., 2013). Furthermore, similarities in personality predict higher quality relationships in capuchins (Morton, Weiss, Buchanan-Smith, & Lee, 2015) and in chimpanzees (Massen & Koski, 2014). One of the criticisms of using the 'subjective' rating method is that it is anthropomorphic to describe animals as having personalities, and we are simply projecting anthropocentric characteristics onto other species (Vazire, Gosling, Dickey, & Schapiro, 2009; Watters & Powell, 2012). However the fact that rated traits correlate significantly with observed behaviours suggests that humans are not simply projecting their own personalities onto the animals they rate, but are in fact able to accurately identify consistent differences between individuals based on their own experience with each animal. The evidence of high inter-rater agreement on trait ratings backs this up, as does evidence from several studies that have assessed the possibility of 'projection' in questionnaire ratings, (Gosling & Vazire, 2002; Kwan Gosling, & John, 2008; Weiss, Inoue-Murayama, King, Adams, & Matsuzawa, 2012). In fact, humans are no more likely to project their personality onto a dog than they are onto another human (Kwan, et al., 2008).

It is somewhat unfortunate that despite this evidence, some researchers still take the view that the ethological approach to assessing individual differences is preferable to using questionnaire ratings. These critics generally have two problems with personality assessment: firstly, they prefer to refer to personality in nonhuman animals as temperament or behavioural types (Watters & Powell, 2012), suggesting that the word 'personality' is a purely human definition. However, we should consider that temperament is a term that has also been applied to studies in human children (Rothbart, 2012). Furthermore, it would seem more anthropocentric of us to consider ourselves completely distinct from other species, than it would be to suggest that we might share ancestral traits and thus, find personality traits in other species that are similar to those found in humans (Dethier, 1964; Gosling, 2001).

The second critique of personality assessments is the use of questionnaires to assess personality (Gosling, 2001). Already I have pointed out that questionnaire ratings correlate with behavioural observations. When it comes to choosing the most appropriate method to assess personality, we should consider what the benefits are of choosing one method over the other. Whilst behavioural observations are useful for assessing very specific behaviours, such as response to a stressor or novel object, the use of questionnaire ratings allows collection from a larger sample (i.e. across multiple zoos) and for behavioural assessment across-contexts (Watters & Powell, 2012). Taken together, the findings described above strongly indicate that questionnaire ratings are a valid method of personality assessment in nonhuman animals that can benefit our understanding of species-specific traits.

Given the above findings – that personality can be rated as accurately in animals as in humans - we can return to the question: why study personality? There are a number of answers to this. Here I will describe three of them.

The first answer is that by studying personality traits in other species, we can understand more about the origins of similar traits in humans, and what selection pressures may have contributed to their evolution. For example, comparing trait structures across the apes has revealed that humans (McCrae & Costa, 1985), chimpanzees (King & Figueredo, 1997; Weiss et al., 2009) and orangutans (Weiss, King, & Perkins, 2006) have a Neuroticism dimension, but bonobos (Weiss et al., 2015) and mountain gorillas (Eckardt et al., 2015) do not. In chimpanzees, the Neuroticism dimension is defined by four items – *(+)excitable, (+)autistic, (-)stable and (-)*cool (Weiss et al., 2009). In orangutans these items also cluster onto Neuroticism (Weiss et al., 2006) and in bonobos and gorillas they also cluster together, albeit onto different dimensions – Assertiveness and Openness, respectively (Eckardt et al., 2015; Weiss et al., 2015). This pattern is suggestive of different selection pressures acting on the prominence of these traits in relation to other traits. For example, perhaps the formation of these traits into a Neuroticism dimension is the result of an unstable social environment where becoming easily aroused allows an individual to react quickly to others. Such that, in groups of relative social stability (such as gorillas) or where conflict is often resolved without aggression (such as bonobos) neurotic traits are less prominent than in species of changing group composition and high intersexual aggression (chimpanzees and orangutans). Examining differences in social structure and habitat of each species thus allows us to build hypotheses as to what selection pressures may drive particular trait structures.

The second answer considers the role of personality in experimental research, which has been studied in nonhuman primates. There are two points to consider here. The first is that of research participation. In chimpanzees and capuchins, individuals higher in Openness tend to have higher participation in cognitive training tasks (Herrelko, Vick, & Buchanan-Smith, 2012; Morton, Lee, &

Buchanan-Smith, Brosnan, et al., 2013). Given that experimental studies in captive primates often tend to rely on those willing to participate (an important welfare consideration in captive research (Schapiro & Lambeth, 2007)), then there is a strong chance that the data is biased from the outset by excluding those who are not willing to participate, for example, individuals lower in Openness. Thus, the resulting data does not reflect the full variation of individual differences within the sample, and thus is unlikely to reflect population level variation. This is particularly important, in light of the second point: that individuals differ in their performance on cognitive tasks. In several species of ape, some individuals consistently perform better than others (Herrmann, Hernandez-Lloreda, Call, Hare, & Tomasello, 2009; Vonk & Povinelli, 2011), an aspect of primate cognition that has largely been ignored up until recently (Herrmann & Call, 2012). In one study, performance on physical cognition tasks in chimpanzees and orangutans – assessing spatial knowledge, quantity discrimination and causal reasoning - was higher for bold rather than shy individuals (Herrmann, Call, Hernandez-Lloreda, Hare, & Tomasello, 2007). Furthermore, recent findings indicate that ratings of personality, including higher Openness, predict better cognitive performance amongst rhesus macaques and brown capuchins (Altschul, Terrace, & Weiss, 2016; Morton, Lee, & Buchanan-Smith, et al., 2013). These findings suggest that there may be similar mechanisms underlying certain aspects of cognition and personality traits (DeYoung, Quilty, Peterson, & Gray, 2014). Thus, addressing the role of specific traits in both participation and performance on such tasks should be made a priority of future studies. The first step towards doing this, of course, is to expand personality assessment to species for whom such data is currently lacking.

The third and final answer that I shall address here – as to why we should study personality in animals – relates to what we know about personality in humans. That is, we know that personality is an important predictor of health, well-being and mortality in people. Thus, assuming these relationships have a biological basis, we would expect similar findings in other species. Yet, research is only just beginning to broach the ways that personality traits influence important life variables in nonhuman animals (Mehta & Gosling, 2008). Below I outline these influences and the potential role that personality can play in elucidating individual differences in survival.

1.2 The Role of Personality in Fitness

1.2.1 Personality in health and well-being.

In humans, personality traits are associated with a number of health outcomes, such as the link between high Neuroticism and risk of respiratory disease; however the exact nature of such relationships is unclear (Deary et al., 2010; Roberts, Kuncel, Shiner, Caspi, & Goldberg, 2007). That is, it is possible that personality could influence health outcomes by, for example, mediating chronic stress responses, or through health behaviours and coping mechanisms (Deary et al., 2010). Personality is also linked to subjective well-being ratings, a self-report measure of happiness; people with higher scores on Extraversion and Conscientiousness, and lower scores on Neuroticism tend to report higher well-being

(DeNeve & Cooper, 1998; Hayes & Joseph, 2003; Schimmack, Oishi, Furr, & Funder, 2004; Steel, Schmidt, & Shultz, 2008b). Given these tentative links between personality, health and well-being, assessment in other species could be beneficial to understanding how such relationships evolved.

Subjective well-being can be assessed in nonhuman primates just as personality can, using keeper ratings on a Subjective Well-being Questionnaire (King & Landau, 2003). Research has found that in ape species, low Neuroticism and high Agreeableness and Extraversion are associated with higher subjective well-being (King & Landau, 2003; Schaefer & Steklis, 2014; Weiss et al., 2009; Weiss et al., 2006). Similar results can be seen in rhesus macaques, with high scores on Confidence and Friendliness and low scores on Anxiety predicting higher well-being (Weiss, Adams, Widdig, & Gerald, 2011). These reflect findings in humans, suggesting that links between personality and well-being are not specific to just humans and may be ancestral amongst primates. Further exploration has revealed that both personality and well-being are linked to longevity in apes: gorillas rated higher on Extraversion, and orang-utans higher on well-being, live longer (Weiss, Adams, & King, 2011; Weiss, Gartner, Gold, & Stoinski, 2013b). It could be that more extraverted individuals rely on the company of others to alleviate stress, and thus mediate physiological stressors, increasing potential life span; alternatively it is possible that extraversion is an indicator of immune function or cardiovascular risk (Weiss et al., 2013). Only further research can help to illuminate causal factors in longevity.

To date, only a few studies have examined the biological correlates of personality. In clouded leopards, fearfulness has been associated with higher faecal corticoid concentrations, which is an indication of chronic stress (Wielebnowski, Fletchall, Carlstead, Busso, & Brown, 2002). Similarly in wild baboons, females who frequently spent time alone tended to have higher glucocorticoid levels, even when accounting for dominance rank (Seyfarth, Silk, & Cheney, 2012). Personality has also been associated with autonomic nervous system reactivity in goats (Briefer, Oxley, & McElligott, 2015): individuals with higher sociability measures showed significantly less variation in heart rate across behavioural contexts, than individuals with low sociability scores. Moreover, personality traits in rhesus macaques have been linked to immune system function: in macaques infected with SIV (simian immunodeficiency virus), frequency of aggression displays six weeks post-infection were associated with reduced production of CXCL9, (a measure of immune response), which is associated with an increase in viral RNA (Capitanio et al., 2008). This suggests that, similar to research in humans, personality in nonhuman primates is associated with health outcomes.

To understand why there is such variance in personality traits, and how these traits are linked to health and well-being outcomes, evolutionary psychologists tend to consider the ancestral environment. One suggestion is that optimal personality traits varied with environment (Nettle, 2006). For example, neurotic traits that evoke vigilant and wary behaviours may be of benefit in a dangerous environment, where caution aids survival; but the same traits could be maladaptive in an environment where there are few risks (Nettle, 2006). This theory posits that differences in localised selection pressures have ultimately maintained heterogeneity across personality traits in the human population. Other theories account for environmental variation differently. For example, selective migration and settler effects may result in localised population differences in trait expression (Rentfrow, Gosling, & Potter, 2008). Within-trait variation could also simply be frequency-dependent, that is, the frequency and benefit of a phenotype is relative to the frequency and benefit of other phenotypes in the population (Bouchard & Loehlin, 2001). Alternatively, within-trait variation could result from cost-benefit trade-offs: for example, an extravert who has multiple sexual partners could increase the genetic variety and number of their offspring, but with potential cost to offspring survival (Nettle, 2005). Understanding the costs and benefits of particular traits could improve our understanding of how personality seems to be so intrinsically linked to health and well-being.

Research in nonhuman animals could thus benefit our understanding not only of the origins of these traits, but also of their role in individual fitness. Such research not only informs evolutionary theory, but also has real-world applications. If we consider the relevance of these findings to captive management, we can begin to understand the importance of personality assessments in captive animals. One of the aims of The British and Irish Association for Zoos and Aquariums is *"to achieve the highest standards of animal care and welfare in zoos, aquariums and in the wild"* (BIAZA, 2016), a mission that is only possible with increasing knowledge of what good welfare is. A suitable enclosure, with enough space, the right substrate and food provided in a manner that encourages natural behaviours and enrichment, are all key components of welfare (Morgan & Tromborg, 2007). However, individuals may differ in their needs, and it as yet unclear to what extent personality plays a role in welfare (Gartner & Weiss, 2013). For example, fearful individuals may fare better with more hiding places in an enclosure (Gartner & Weiss, 2013). It has also been suggested that naturally semi-solitary animals such as wild cats may fare better in social housing in captivity, if they are of an agreeable nature (Gartner & Weiss, 2013), given that pair housing can increase natural behaviours even in semi-solitary species (De Rouck, Kitchener, Law, & Nelissen, 2005). Group housed individuals also respond differentially to visitor density: in Diana monkeys, individuals that exhibited aggressive, irritable or solitary traits had increased levels of abnormal behaviour during high visitor density, whereas those that were active and playful showed an increase in species-typical behaviours, such as play (Barlow, Caldwell, & Lee, 2006). Given that well-being is a key consideration in welfare assessment, the associations of personality with well-being have important implications for improving captive welfare conditions.

The current welfare approach tends towards the needs of the group rather than the needs of the individual. Whilst this is of course necessary when caring for a population, it means that individual needs may get neglected, and individuals may suffer as a result. Thus, understanding the differential needs of individuals in a group is important to maintaining wild-type behaviours in captive populations and maximizing breeding programs (Watters & Powell, 2012), two things that are both key to the BIAZA mission (2016), "*to participate in effective co-operative conservation programmes*".

1.2.2 The genetics of personality.

Research to date indicates that personality traits are diverse across species, that 'optimal' personality traits may depend on both the social and physical environment, and that personality has links to physiological processes and health and well-being outcomes. One approach to understanding these concepts in more detail is to examine the genetic basis of personality traits. Since personality traits are partly heritable (van Oers, de Jong, van Noordwijk, Kempenaers, & Drent, 2005) it is important to understand to what extent genes contribute to behaviour.

In nonhuman animals, these studies typically focus on assessing the links between particular traits and polymorphism of target gene regions that play a role in neurotransmission and receptor activity (Inoue-Murayama, 2009). Study of the pathways between gene and protein can determine where changes to the gene results in changes to the protein (Kroslak et al., 2007; Lesch et al., 1996; Vallone, Picetti, & Borrelli, 2000; Van Tol et al., 1992). The building blocks of proteins – amino acids – are made up of codons, consisting of three base pair nucleotides. A non-synonymous Single Nucleotide Polymorphism (SNP) results in a change to the amino acid, which can cause functional differences in the proteins. For example, the codon CTT codes for amino acid leucine. If the Cytosine nucleotide is exchanged for a Guanine nucleotide, the resulting amino acid – GTT – is valine. Thus target gene studies focus on examining minute changes at the genetic level, but these changes have potentially large consequences at the structural and functional level. Target gene research also examines changes to the gene function resulting from variable number tandem repeats (VNTRs), a short nucleotide sequence that is repeated in tandem, the length of which may vary between individuals, resulting in alleles of differing lengths. Many behavioural studies examine whether possessing different combinations of these alleles, such as being a homozygote for the long allele versus being a heterozygote (having one long and one short allele), is associated with differences in behavioural trait expression. By understanding the role of a neuropeptide in neural and physiological processes, theory driven research can build a priori predictions to assess whether changes to the gene and resulting protein produce changes at an observable behavioural level (Tabor, Risch, & Myers, 2002).

The neuropeptide vasopressin is a good example of this. Arginine vasopressin is involved in the regulation of the hypothalamic-pituitary-adrenal (HPA) axis, part of the endocrine system that, amongst other functions, is involved in the regulation of mood and emotion. Changes in reactivity to the HPA axis have been implicated in changes to levels of agonism and group cohesion. Such changes have been observed under domestication. For example, compared to their wild ancestors (*Cavia aperea*), domesticated guinea pigs (*Cavia aperea* f. *porcellus*), which are bred for decreased aggression and increased social tolerance, have reduced reactivity of their pituitary-adrenocortical system (Künzl & Sachser, 1999). The self-domestication hypothesis proposes that processes similar to domestication have taken place in wild animals too (Hare, Wobber, & Wrangham, 2012). For example, when bonobos and chimpanzees diverged, bonobos experienced less competition for resources compared to chimpanzees, leading to reduced aggression. This theory proposes reduced reactivity of the hypothalamic-pituitary-adrenal axis in association with changing selection pressures on behaviour. Compared to chimpanzees, bonobos exhibit morphological differences, such as reductions in canine size (reduced need for weaponary in combat) and other behavioural changes observed in bonobos such as increased adult play and sexual behavior (Enomoto, 1990; Hare et al., 2012). Thus, comparing the chimpanzee and bonobos one million years after they first diverged, the physical and behavioural differences between the two species are apparent.

Understanding of the pathways in which vasopressin is involved has led to an abundance of research examining associations with behaviour. There are three vasopressin receptors, however only two of these have been implicated in social behaviour (Bielsky, Hu, Szegda, Westphal, & Young, 2004; Caldwell, Lee, Macbeth, & Young Ill, 2008; Wersinger, Ginns, O'Carroll, Lolait, & Young, 2002). Primarily, research has focused on behavioural links to the AVPR1a receptor. In Syrian hamsters (*Mesocricetus auratus*) scent marking is higher in high ranking individuals. Vasopressin injections into the medial preoptic area led to increases in scent marking up to forty times that of scent marking following control injections (Ferris, Albers, Wesolowski, Goldman, & Luman, 1984), suggesting that vasopressin is involved in regulating dominance-associated behaviours. Furthermore, oral administration of AVPR1a antagonists inhibited male aggression, showing a thirteen-fold decrease in number of bites and a nine-fold increase in latency to bite for a 2mg dose compared to control (Ferris et al., 2006a). Similar studies have examined the role of vasopressin in modulating behavioural pathways in humans. For example, intranasal administration of vasopressin increased salivary cortisol 1.26 times more than placebo during social stress (Ebstein et al., 2009), and was associated with a 10% increase in reciprocity of cooperation in men compared with placebo trials (Rilling et al., 2012). Similarly, participants receiving intranasal administration of vasopressin exhibited enhanced encoding of negatively valenced facial expressions 1.2 times that of encoding during placebo trials (Guastella, Kenyon, Alvares, Carson, & Hickie, 2010).

Building on this, several studies have addressed links between AVPR1a polymorphism and social behaviour. Men who are carriers of the RS3 334 bp allele of AVPR1a scored lower on a scale that assessed affiliation towards and time spent with their partner (Walum et al., 2008). The RS3 region has also been linked to traits of social appropriateness and sibling conflict (Bachner-Melman et al., 2005), and long forms of the RS3 region (i.e. 327-343 bp) have been associated with higher levels of AVPR1a mRNA in the hippocampus (Knafo et al., 2008). The RS3 microsatellite occurs within the Dup B region of the vasopressin receptor gene in humans (Thibonnier et al., 2000), and as in other great ape species is accompanied by the Dup A region (Donaldson et al., 2008; Hammock & Young, 2005). Chimpanzees however are polymorphic for an RS3 deletion at the Dup B site (Donaldson et al., 2008; Hammock & Young, 2005), that is, some individuals possess an allele in which the RS3 microsatellite is absent. This makes them, as a nonhuman primate species, a suitable candidate for assessment of AVPR1a links to behaviour. By assessing the links between specific polymorphic regions and behavioural traits, we can determine to what extent changes in the gene result in functional differences in the associated pathways.

Hopkins, Donaldson, and Young (2012) found that among chimpanzees who possessed the long form of the Dup B allele, males scored higher than females on the personality domain Dominance and lower on the personality domain Conscientiousness. Male chimpanzees who lacked the Dup B deletion also demonstrated stronger social responsiveness than males homozygous for this deletion (Hopkins et al., 2014). Further research by Anestis et al. (2014) found that chimpanzees with a copy of the L allele (lacking the RS3 deletion) had higher scores on “smart” (“uses coalitions”, “receives grooming often”, “frequently initiates play”) and in males, higher scores on “friendly” (“directs affiliative behaviour to others”) (see their Table II). Similarly, Staes et al. (2015) reported that male chimpanzees homozygous for the long allele, and female heterozygotes, groomed and were groomed by others more frequently. Most recently, colleagues and I examined the relationship between personality and the Dup B polymorphism in a study that controlled for both subspecies and relatedness of subjects. We found evidence for an association between higher Conscientiousness and the long form of the AVPR1a gene (Wilson et al., in press)[2] (see Appendix D). Conscientiousness has been associated with lower aggression in captive chimpanzees (Pederson et al., 2005), suggesting that our results, consistent with earlier findings, indicate an association between the long allele and prosocial behaviour (Anestis et al., 2014; Staes et al., 2015).

Although results from four different studies all associated AVPR1a polymorphism with variation in social behaviour, the variability in these findings

---

[2] The data in this paper were provided by M. Inoue-Murayama and A. Weiss. I conducted the analyses with the help of A. Weiss and wrote the majority of the paper, with suggestions and edits from A. Weiss and other co-authors.

only highlights the problem of heterogenous methods and the need for further replication. In humans, research into specific gene-behaviour relationships has formed a large enough body of work to warrant meta-analysis. Where a single study may be limited in what it can tell us about links between genes and behaviour, meta-analysis allows a more rigorous assessment of these associations.

The gene for the dopamine receptor (*DRD4*), a protein that is involved in the neural transmission of the neuropeptide dopamine, has been repeatedly associated with novelty seeking in humans. Two meta-analyses have examined these associations in detail, assessing several gene regions. Schinka, Letsch, and Crawford (2002) examined a sample of 2720 subjects from 22 studies. For each study, effect size (*d*) is calculated as the mean difference in novelty seeking score between groups with different genotypes, divided by the standard deviation of both groups. Mean *d* is then calculated across all studies. For the -521 C/T promoter polymorphism, a mean effect size of 0.32 (*SD* = 0.14) was reported. Although the link between this polymorphism and novelty seeking was only assessed in four studies, these results were the most promising of a relationship between DRD4 polymorphism and novelty seeking. Munafo, Yalcin, Willis-Owen, and Flint (2008) found similar evidence in a meta-analysis of 48 studies. In a subset of 11 studies, the effect size was 0.25 for an association of novelty seeking with the -521 C/T promoter polymorphism. Results indicated that possession of the T allele was associated with lower scores on novelty seeking.

These findings encourage further research into target gene-behaviour associations. However, the validity of target gene studies has become a hotly debated area, with the suggestion that genome wide association studies (GWAS) are a more suitable alternative, because they account for the fact that behavioural traits may be influenced by small effects of multiple genes (Chabris et al., 2012; Munafo & Flint, 2011). Particular criticism is given to the lack of power many studies have. One review found that, to get an effect size of 0.2, they needed at least 390 subjects in their sample (Munafo et al., 2003). However, it is argued that careful a priori predictions in target gene studies should decrease the potential for false positives and low replicability, one of the primary concerns of this field (Tabor et al., 2002). Furthermore, the application of meta-analyses to this field helps to boost limited power and account for heterogeneity of methods across studies. Thus research should continue to address how these functional differences implemented at the genetic level link to differences in behaviour and physiology, especially in nonhuman species where the challenges of large sampled GWAS are impractical.

An additional and important consideration when addressing the genetics of personality is the role that the environment plays in the link between gene and behaviour. Epigenetics is the assessment of changes in gene expression, which can be influenced by the environment (Holliday, 2006; Feinberg & Fallin, 2015). In human research, twin studies have revealed that personality and behavioural traits appear to be partly heritable (Johnson & Krueger, 2004; Knafo-Noam, Uzefovsky, Israel, Davidov & Zahn-Waxler, 2015; Polderman et al., 2015), indicating that variation in personality results in part from environmental effects too. A review of heritability estimates for the five dimensions of human personality found them to vary between 0.33 and 0.61 (Bouchard & Loehlin, 2001). Similar effects are found in assessment of nonhuman primates. For example, chimpanzee Dominance was estimated to have a heritability of 0.63 (Weiss et al., 2000). Nonhuman research has been important in understanding environmental effects on behaviour. For example, assessment of response to SIV infection in rhesus macaques found that individuals heterozygous for the serotonin transporter promoter region exhibited more aggression under an unstable social environment compared with a stable social environment, six weeks post-inoculation (Capitanio et al., 2008). Early life rearing condition can have a significant effect on neurobehavioural development (Bard, Brent, Lester, Worobey, & Suomi, 2011). Suomi (2006) found that early social rearing influenced later behavioural outcomes in rhesus macaques with a short copy of the serotonin transporter gene, but had no effect for those with the long allele. Those with the short allele which were peer-raised showed delayed neurobiologoical development, impaired serotonergic function and excessive aggression compared to their mother-reered peers with the same allele. These findings highlight the importance of accounting for the environment in the consideration of associations between genotype and behaviour.

1.2.3 Morphological correlates of personality.

Given the links of personality to hormonal expression (e.g. links between fearfulness and higher corticoid production; associations between dopamine expression and novelty seeking (Munafo et al., 2008; Schinka et al., 2002; Wielebnowski et al., 2002)) it is appropriate to consider that certain traits also have morphological markers. Recent work in humans has examined the face as a signal of dominance and aggression. To understand the theory behind this approach, I will first address the more general role of the cranio-facial region in behaviour.

Cephalisation is the process that refers to the concentration of neural cells at one end of the body of multicellular organisms, leading to the formation of ganglia and furthermore, brains (Striedter, Avise, & Ayala, 2013; Weinstein, 1995). This is an evolutionary ancient trait that has occurred throughout invertebrate and vertebrate species, and varies morphologically from simple nerve nets in cnidarians up to the complexity of functionally varied brain regions seen in mammals (Weinstein, 1995). In conjunction, sensory organs evolved cephalically, allowing features of mechanoreception, light detection, olfaction, chemoreception and sound perception to be detected by nearby neural cells. In vertebrates, the head has become a particularly specialised region, with distinct morphological and functional features, including facial musculature and neural structures (Gans & Northcutt, 1983; Sambasivan, Kuratani, & Tajbakhsh, 2011). How the craniofacial region became so specialised remains unclear (Sambasivan et al., 2011). Yet the opportunities of niche-exploitation provided by advanced craniofacial features, such as communication and cognition, were likely a driving force for its selection.

Indeed, the face has been a much studied region in understanding vertebrate social behaviour and communication. In humans the face communicates emotional expression, which can be measured using the Facial Action Coding System, a system that discerns individual facial movements and their associated musculature (Ekman & Friesen, 1971; Ekman & Friesen, 1978). Comparative assessment has found that homologous facial expressions (Parr, Waller, & Fugate, 2005; Waller & Dunbar,

2005) and underlying musculature (Parr, Waller, Vick, & Bard, 2007; Vick, Waller, Parr, Pasqualini, & Bard, 2007) exist in chimpanzees. Similar expressions are also seen across both Old World and New World primates, some of which exhibit behavioural similarities between species. For example, the relaxed open mouth display appears to be most associated with play behaviour in chimpanzees (*Pan troglodytes*) (Waller & Dunbar, 2005), Barbary macaques (*Macaca sylvanus*) (Preuschoft, 1992) and brown capuchins (*Sapajus apella*) (Visalberghi, Valenzano, & Preuschoft, 2006). In contrast, the behavioural context of some facial displays varies between species. The silent bared teeth display, in rhesus (*Macaca mulatta*) and Barbary macaques (Preuschoft, 1992; Van Hooff, 1976) is primarily seen in lower ranking individuals as a response to aggression from dominants. However in more egalitarian species such as chimpanzees[3] (Waller & Dunbar, 2005) and capuchins (Visalberghi et al., 2006) it may be seen in multiple contexts such as submission, affiliation and play, suggesting benign intent and perhaps being used to create appeasement and affiliation (Parr & Waller, 2006).

The fact that the face plays such a strong and complex role in the communication of emotions is an important consideration for addressing both species and individual differences in social interactions. Indeed, this role may go beyond the communication of just emotions, to act as a signal of personality. Of course, personality does not occur independently of emotion, but the consideration that we may still read certain traits from a neutral expression is an intriguing one. Research in humans has become extensive in assessing the links between facial

---

[3] The evidence that chimpanzees are egalitarian is mixed

morphology and personality. A ratio of face width to height – the facial Width to Height Ratio (fWHR) – has been associated with aggression (Carré & McCormick, 2008) and achievement striving (Lewis, Lefevre, & Bates, 2012) in males, with wider faces scoring higher on these behaviours. Although associations between facial morphology and dominance-related behaviour have been questioned (Deaner, Goetz, Shattuck, & Schnotala, 2012), recent studies continue to support earlier findings (Haselhuhn, Ormiston, & Wong, 2015; Trebicky et al., 2015; Zilioli et al., 2015). Furthermore, the relationship between face width and dominant-associated traits appears to be mediated by testosterone, with both baseline and reactive testosterone levels during potential mate exposure being highest for those in the top quartile of fWHR (Lefevre et al. 2013).

In humans, aggression can be predicted from the face (Lefevre & Lewis, 2013), as can trust and cooperation (Stirrat & Perrett, 2010), dominance (Alrajih & Ward, 2014) and success (Alrajih & Ward, 2014; Mileva, Cowan, Cobey, Knowles, & Little, 2014). For example, fWHR of facial images accounted for 16% of the variation in rated trust of those images, with wider faces percieved as less trustworthy (Stirrat & Perrett, 2010). Wider male faces (width adjusted by +50%) were also more than twice as likely to be rated as dominant then comparable images of narrower faces (width adjusted by -50%) (Lefevre & Lewis, 2013). And of male facial images, those that depicted CEOs were percieved as 1.16 times more dominant, and 1.3 times more successful, than a control group depicting non-CEOS, who had a lower average fWHR than the CEO group. Taken together, these finding suggest that the face acts as a signal of traits associated with dominance.

The reasons for this remain elusive. Signals[4] may act as ‘honest’ indicators of fitness; it has been suggested that masculinity in the human face is a signal of immune function (Thornhill & Gangestad, 2006). However face width may alternatively be a useful signal for recipients to avoid direct conflict with someone they perceive as more aggressive. Such avoidance behaviour can be seen in other species, for example the increased use of the bared-teeth displays in macaques living in crowded conditions (Judge & de Waal, 1993), and the use of ritualistic fighting behaviour to avoid serious injury (Eibl-Eibesfeldt, 1961).

It is possible that in nonhuman primates, canine size acts as a signal of fitness. Weston, Friday, Johnstone, and Schrenk (2004) proposed that canine size and fWHR are sexually dimorphic traits that are inversely related to each other at the species-level; for example, capuchins *Sapajus apella* are highly dimorphic on fWHR but show low dimorphism on canine height (Weston et al., 2004). These differences likely occurred through sexual selection, although the reasons for such interspecific variation are not clear; it is proposed that exploring behavioural associations of these features may prove valuable to understanding these traits further (Weston et al., 2004). This could help to establish whether the associations of personality with a facial metric are unique to humans. It could also tell us, more generally, about the role of the primate face in social communication and interaction, which in turn could benefit our understanding of personality in relation to social interactions.

---

[4] For a more detailed discussion of signals, please see Chapter 6

1.3 The Integration of Personality into a Broader Research Framework

To conclude an earlier question – why study personality? – I would like to draw upon the examples here as evidence for both the breadth of variables in which personality plays a role, and for the need for applied work that takes the individual into account. We now know that personality is associated with social behaviour, is related to well-being, has a genetic and physiological basis as well as morphological correlates, and has been studied in numerous species, both primate and non-primate. Despite this growing wealth of knowledge, there are a number of holes in the current research literature that I aim to address in this thesis. The first is to build on comparative work assessing personality and well-being in apes and Old World monkeys, by extending assessment to South American squirrel monkeys. The second aim is to expand our understanding of how personality relates to social interactions and socio-emotional perception in our closest relatives, chimpanzees. The third aim is to extend assessment of personality and facial morphology from humans to nonhuman primates, by examining these associations, and perceived associations, in brown capuchins. By taking a multi-species approach, I hope to highlight new directions for understanding the role of personality in socio-emotional behaviour.

I have discussed above the associations of personality with behaviour, well-being and morphology. As the literature on emotional perception is somewhat disparate, the second half of this chapter will introduce the study and definition of emotional perception, focusing on chimpanzees. In addition to clarifying definitions and discussing the reasons for this research, I will argue that taking a differential approach to assessing emotional perception can be beneficial to its assessment.

1.4 Emotional Perception

"The ability to understand emotion in others is one of the most important factors involved in regulating social interactions in primates."
- Lisa A. Parr (2001, p. 223)

1.4.1 The definition of emotional perception.

Lisa Parr puts in succinctly. Emotional perception is a key part of social interaction, with potential welfare implications for captive animals (Edgar, Nicol, Clark, & Paul, 2012). This makes it an important consideration for understanding social interactions, and moreover, for the study of personality in relation to social behaviour. Yet, it is an area that lacks thorough understanding and furthermore, is under researched.

In order to test emotional perception, we first need a solid and consistent definition of this term. However the definition of emotional perception shows vast variation throughout the literature. The difficulty here is that emotional perception can refer to multiple layers of perception, and envelopes a rather broad range of abilities. Thus it is more of an umbrella term for empathy and related behaviours. de Waal (2008) did a thorough job at addressing inconsistencies and honing definitions, yet the research on emotional perception is still disparate and often lacks clarity. Here I try to address these definitions, and outline my own definitions drawn from the literature, using de Waal (2008) as a guide.

The perception of emotions in conspecifics starts from very early on in human infants, but as with other socio-cognitive skills, changes and develops with age (see Table 1.2). Perhaps the most basic form of emotional perception is emotional contagion. Contagion is a process of emotional transfer, whereby expression in one individual can invoke expression of the same emotion in another (Hatfield, Cacioppo, & Rapson, 1994). Contagion is primarily reflexive and can result in emotional arousal and physiological changes, such as changes in skin temperature (de Waal, 2008; Parr, 2001). It is thus an automatic and unconscious process. Examples of emotional contagion have been observed in newborn infants, who will cry in response to the cry of another infant (Simner, 1971). In infant chimpanzees too (from 11 weeks old), physiological responses are observed in response to conspecific vocalisations, including deceleration of heart rate upon hearing screams, and acceleration of heart rate upon hearing laughter (Berntson, Boysen, Bauer, & Torello, 1989). In fitness terms, adopting the emotional and behavioural state of a conspecific is likely advantageous in many instances; for example, a flock of birds taking flight or monkeys repeating the alarm call of a conspecific. Relying on cues of conspecifics to flee predation aids survival (de Waal, 2008).

A lot of emotional processing can take place outside of conscious awareness (Hatfield et al., 1994). Whilst emotional contagion is our most basic response to emotional contexts (de Waal, 2008) it is not the only unconscious process happening in emotional perception. From only four days old, human infants are able to recognise their mother’s face (Pascalis, de Schonen, Morton, Deruelle, & Fabre-Grenet, 1995). Face to face interaction is a critical part of the mother-infant bond (although mother-infant interactions vary across cultures; see for example Tronick, Morelli and Winn (1987)), and mutual gaze plays a strong role in this (Emery, 2000). Chimpanzee infants also show recognition for their mother's face, between four and eight weeks old (Myowa-Yamakoshi, Yamaguchi, Tomonaga, Tanaka, & Matsuzawa, 2005) and infants use emotional expression to interact with care givers (Bard, 1998). From the age of three months, human infants can discriminate gaze direction and by six months will follow another's gaze (Butterworth & Jarrett, 1991; Farroni, Johnson, & Csibra, 2004). Infant chimpanzees are able to discriminate direct from averted gaze from 10 weeks old (Myowa-Yamakoshi, Tomonaga, Tanaka, & Matsuzawa, 2003), although gaze following seems to develop later than in humans, between 11 and 13 months old (Okamoto et al., 2002). Trevarthen (1979) describes this development period as 'emotional intersubjectivity' - the ability to attune to another using eye gaze and facial expression. 'Subjectivity' refers to how we perceive the world around us, that is, our own subjective experience; thus intersubjectivity describes our ability to perceive the subjectivity of others (Gomez, 1998). Emotional intersubjectivity is a two-way process, such as the exchange of emotions between an infant and its carer; it is thought to be present in infants as young as three months old, and allows emotional perception to take place without the need to induce conscious awareness (Trevarthen, 1979).

Table 1.2

Developmental stages of Theory of Mind in humans and chimpanzees

Level of Perception	Presence/Age of occurrence in humans	Presence/Age of occurrence in chimpanzees	Developmental Stages	Level of Awareness
Emotional contagion	Present at birth[1,2]	Present in young infants[3]		Unconscious
Recognition of mother's face	As young as 4 days old[4]	By 1 month old[5]		
Mutual gaze	Present[6]; increases as physical contact decreases[7]	Present; increases as physical contact decreases[8]	Emotional Intersubjectivity[18]	
Discriminate gaze direction	By 3-4 months[9]	By 11-13 months[10]		
Gaze following	Around 6 months[11]	By 13 months[12]		
Joint attention	Around 6 months[11]	Around 1 year old[8]		
Triadic interactions	Evident around 9 months[6,13]	Mixed evidence[8,14]	Intellectual Intersubjectivity[18]	Conscious
Understanding intent	By 4 years old[15]	Yes[16]	Theory of Mind[19]	
False belief	By 4 years old[17]	No evidence[16]		

Note. [1] Hatfield et al. (1994); [2] Simner (1971); [3] Berntson et al. (1989); [4] Pascalis et al. (1995); [5] Myowa-Yamakoshi et al. (2005); [6] Emery, (2000); [7] Lavelli & Fogel (2002); [8] Tomonaga et al. (2004); [9] Farroni et al. (2004); [10] Myowa-Yamakoshi et al. (2003); [11] Butterworth & Jarrett (1991); [12] Okamoto et al. (2002); [13] Carpenter et al. (1998); [14] Russell et al. (1997); [15] Baron-Cohen (2001); [16] Call & Tomasello (2008); [17] Wimmer & Perner (1983); [18] Trevarthen (1979); [19] Premack & Woodruff (1978).

Whilst it would be parsimonious to assume that emotionally contagious and intersubjective behaviours explain much of emotional perception, in some cases of social interaction, more complex perception processes are required. From six months old, infants develop joint attention (Butterworth & Jarrett, 1991), where they will follow another's gaze to a particular object. This is the pre-requisite for triadic interactions, beginning with shared attention occurring around nine months old (Carpenter, Nagell, Tomasello, Butterworth, & Moore, 1998; Emery, 2000). Although not all researchers make the distinction between shared and joint attention, shared attention is considered to be a more advanced form of joint attention in that it requires mutual knowledge between two people that they are both looking at the same object (Emery, 2000). At this stage, infants will begin to interact with their carers by showing or requesting objects (Carpenter et al., 1998). Joint attention does appear to occur in infant chimpanzees (Bard & Leavens, 2009). For example, one year old infants have been observed to jointly engage with a novel object alongside their mothers (Tomonaga et al., 2004). However, evidence for shared attention in chimpanzees is mixed. Chimpanzee infants have been observed to glance back towards human carers when interacting with a novel object (Russell, Bard, & Adamson, 1997) but other research has found that infants tend not to show or give objects to their mothers when interacting with them, a crucial part of triadic interactions in humans (Tomonaga et al., 2004).

The development of triadic interactions leads to more complex perspective taking abilities. From the age of four children learn to assess the intent, knowledge, beliefs, desires and feelings of others, and to understand false belief, a set of abilities termed Theory of Mind (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001; Premack & Woodruff, 1978; Wimmer & Perner, 1983). Another term for this developmental period, starting from the development of triadic interactions at nine months, is 'Intellectual intersubjectivity' (Trevarthen, 1979). From this age, children begin to partake in team-work and understand perspective taking (Baron-Cohen et al., 2001; Emery, 2000b; Trevarthen, 1979), and social responses are considered to be learned and are generally conscious (Trevarthen, 1979).

There has been much debate as to whether Theory of Mind is specific to humans; current evidence suggests that chimpanzees can understand the knowledge and intent of others, but fail to grasp false belief, suggesting that they share some but not all elements of human perspective taking (Call & Tomasello, 2008). Importantly, most research assessing Theory of Mind in nonhuman primates has focused primarily on knowledge understanding, i.e. assessing what others know (Call & Tomasello, 2008; Crockford, Wittig, Mundry, & Zuberbuhler, 2012; Drayton & Santos, 2016; Hirata, 2009). It is still not clear as to what extent chimpanzees perceive, and empathise with, emotions in others.

Work by Parr and colleagues (Parr, 2003) explored how chimpanzees respond to emotional expressions in the facial images of conspecifics. They found that chimpanzees recognise conspecifics from photos (Parr & Hopkins, 2000), can identify different facial expressions from images (Parr, Hopkins, & de Waal, 1998) and can correctly associate specific expressions with scenes of positive or negative valence (Parr, 2001). This demonstrates that chimpanzees can recognise and understand the context of emotion, which suggests that they may also have the ability to understand emotional perspectives. However, to perceive an emotion of a conspecific is not necessarily to show empathy for that conspecific, even when interest is shown (Edgar et al., 2012).

The term empathy has been defined in a number of ways, so at this stage it is important to be clear what I mean by empathy. Here I take de Waal's definition, that empathy involves not only the recognition of an emotional state in a conspecific, but also a change in one's own bodily state to match that of the conspecific (de Waal, 2008). Although the two terms are often confused, empathy is differentiated from sympathy, in that sympathetic concern is a response to a conspecific's emotional state that involves reassurance behaviour, but not necessarily a change in one's own emotional state (de Waal, 2008; Wispé, 1986). For example in humans, we can be sympathetic towards someone's feelings, without feeling what they feel.

In humans, empathy is generally considered to include perspective taking (Decety & Jackson, 2004). However this is not necessarily always the case; patients with lesions in the inferior frontal gyrus can understand the perspective of another, but lack feeling for them (Shamay-Tsoory, Aharon-Peretz, & Perry, 2009). Similarly, in nonhuman species, empathetic behaviours may occur without perspective taking (although not all researchers make this differentiation, such as Morimoto and Fujita (2011)). For example, offering reassurance to a conspecific could demonstrate empathy, but this behaviour could just as easily be the result of an emotionally contagious response, for example, consoling another may also provide self-reassurance (Koski & Sterck, 2007).

Recent evidence points to the suggestion that there are separate neural systems in humans for emotional empathy and perspective taking (Shamay-Tsoory, 2011; Shamay-Tsoory et al., 2009) which could explain why there is such behavioural variation associated with emotional perception. Thus, it is all the more important that we define what we mean by empathy. If we view empathy as a perspective taking process – that is, the ability to understand the emotional state of another and the reasons and context for these emotions – then we should refer to it as 'cognitive' empathy (de Waal, 1996), an ability akin to Theory of Mind. This differs from 'emotional' or affective empathy, because theoretically, empathy – emotion recognition, change in body state – can occur without taking any perspective into account. These segregations and differences in types of emotional perception suggest a layered process, whereby more complex socio-cognitive processes (e.g. perspective taking) build on lower level, reflexive responses (e.g. emotional contagion). This onion-like layering system is presented as a Russian doll model of empathy and imitation (de Waal, 2008). At its core, the 'inner' doll features emotional contagion and motor mimicry. The next layer contains sympathetic concern, consolation, coordination and shared goals. The final, outer layer includes perspective taking, targeted helping, imitation and emulation.

Based on this layering system, and the definitions outlined above, I refer to emotional perception as an umbrella term for all forms of emotional recognition and response, from automatic, non-conscious processes to those possibly involving perspective taking (Shamay-Tsoory, 2011). Within this umbrella term I define five levels of response (see Table 1.3).

Table 1.3

The five levels of emotional perception

Response levels	Definition
Emotional contagion/arousal	Automatic response resulting in physiological changes and behavioural alteration; contagion involves matching the state of a conspecific
Emotional awareness/recognition	Acknowledging an emotion via gaze and showing recognition of that emotion through choice of response
Sympathetic concern	Offering reassurance/consolation to a conspecific
Emotional empathy	Matching the emotional state of a conspecific and recognising the emotion
Cognitive empathy	Understanding the emotional perspective of a conspecific and the causes of that emotional state

Note. Each 'level' is not an isolate process and may function in conjunction with other levels. Notably, emotional empathy requires both emotional contagion and emotional recognition to take place.

These definitions should not imply that each level is a singular, detached response with no relation to its neighbouring level; on the contrary, these different aspects of emotional perception likely come together as a package of responses in any given combination. For example, a chimpanzee witnesses a conflict in two conspecifics: they may show *awareness* of the conflict by looking towards it or moving towards or away from it, depending on whether they want to join in, or avoid the conflict. They will likely experience *emotional arousal* as a contagious, automatic response – a change in heart rate, skin temperature, piloerection (hair standing on end); a contagious response may pass through the group, with other conspecifics experiencing similar arousal behaviours. Behaviourally, this response may predominate, however *consolation behaviour* may also result following the conflict.

These three levels of perception are observable and therefore relatively straight forward to collect data on. However, determining the fourth and fifth levels of emotional perception – *emotional empathy,* and *cognitive empathy* – is more difficult. In a group setting, how can we tell if a chimpanzee can understand a conspecific's perspective, or whether they experience emotional empathy? Thus assessing this level of perception is reliant on some form of test that can determine whether an individual is able to take a certain perspective.

Given the ready body of knowledge available on chimpanzees' Theory of Mind, empathetic abilities and socio-emotional development (Call & Tomasello, 2008; Hirata, 2009; Bard et al., 2014), chimpanzees are an ideal study species in which to extend the study of emotional perception. So what is the evidence for these different levels of emotional perception in chimpanzees? There are numerous anecdotes describing empathetic behaviours (O'Connell, 1995), but empirical assessments of empathetic behaviour are few. Emotional contagion is evident in chimpanzee social groups during conflict, feeding and displays. Chimpanzees show arousal through changes in heart rate in response to vocalisations (Berntson et al., 1989) and conflict footage (Kano, Hirata, Deschner, Behringer, & Call, 2016), and in brain, skin and face temperature changes in response to emotional stimuli (Parr & Hopkins, 2000; Parr, 2001; Kano et al., 2016). Evidence from touch screen tasks also shows that chimpanzees are able to discriminate between different emotions

(Morimura & Matsuzawa, 2001) and can recognise emotional expressions and contexts (Parr, Hopkins & de Waal, 1998; Parr, 2001).

Studies examining post-conflict behaviour have helped our understanding of empathetic behaviours, showing that chimpanzees engage in consolation behaviour, which is thought to reflect sympathetic concern (Romero, Castellanos & de Waal, 2010). Consolation may act to alleviate stress (de Waal & van Roosmalen, 1979; Fraser et al. 2008), although others refute this argument (Koski & Sterck, 2007). Research has shown that a third party member is more likely to show consolation towards the victim of a fight than the attacker (de Waal & Aureli, 1996), suggesting that not only do chimpanzees display emotional empathy, but that they are capable of taking perspective through the use of targeted consolation. However consolation is more likely to occur between kin or individuals with valuable relationships (Fraser, Stahl & Aureli, 2008; Romero et al., 2010), suggesting that consolation may benefit the giver as much as the receiver, for example through strengthening social bonds. Thus if consolation behaviour is related to giver benefits, it may not function as a result of perspective taking, thus we should be cautious about interpreting consolation behaviour to indicate cognitive empathy.

Further evidence on emotional perspective taking comes from studies of helping behaviour. de Waal (2008) describes a situation where a mother chimpanzee responds to the cries of her infant by offering it assistance, suggesting this is evidence for empathetic perspective taking, as the mother is responding not only to the emotional situation of the infant, but also to the difficulty, by providing a solution. Hirata (2009) points out that such a response could be due primarily to an emotional reaction, that is, emotional contagion (the mother also feels distressed) and sympathetic concern (wants to reassure her offspring) thus result in helping behaviour. In contrast, a situation where a mother offers her infant assistance in the absence of an emotional response (such as choosing to carry the infant before a lengthy journey) suggests that she can consider the perspective of her offspring even when emotional expression is not involved.

Helping behaviour has been studied in chimpanzees under some experimental conditions, producing mixed results. When chimpanzees can preferentially choose to give food to non-kin at no cost to themselves, they fail to show a significant difference in behaviour on the task between conditions when a conspecific is present and absent (Silk et al., 2005). This study suggested that chimpanzees are only willing to cooperate with kin. However, other research has found that chimpanzees will share food with non-kin if those conspecifics request food (Melis et al., 2010), and also tend to respond to a conspecific's request for a tool when they themselves do not need it (Yamamoto, Humle & Tanaka, 2009). Thus far, results suggest that chimpanzees can help others, but do not necessarily choose to. This proposes the idea that chimpanzees do understand conspecifics' perspectives, but do not necessarily empathize with them, supporting the notion of separate systems for emotional empathy and cognitive empathy (Shamay-Tsoory et al., 2009; Shamay-Tsoory, 2011). Alternatively, it is possible that, as with Theory of Mind studies (Call & Tomasello, 2008), chimpanzees' abilities to understand the emotional perspectives of others are limited. This leaves open the question as to whether chimpanzees really can take emotional perspectives into account.

1.4.2 Taking a differential approach to emotional perception.

The ability to recognise, empathise with, and understand the emotions of others is a key part of human social behaviour. We know that very similar behaviours occur in chimpanzees, yet based on the literature discussed above, we still do not know the full extent of these behaviours. One way to examine emotional perception in more detail is to examine how individuals differ in their ability to perceive the emotions of others. Recent research into chimpanzee post-conflict behaviour indicates that individuals consistently differ in the extent to which they reconcile with others (Webb, Franks, Romero, Higgins & de Waal, 2014). A personality framework provides a novel approach through which to understand such individual differences in chimpanzees, and should prove useful when applied to assessing emotional perception.

Personality is an important predictor of responses across contexts, and predicts differences in social behaviours: in captive brown capuchins, those high in Neuroticism spend less time grooming with conspecifics (Morton, Lee & Buchanan-Smith, 2013). Findings in wild primates suggest that these are not just products of captivity, and that personality influences social interactions in the wild too. Female chacma baboons most frequently approach other females who are friendly (i.e. how often they touched or embraced others) and are less likely to approach conspecifics who are frequently aggressive or tend to spend time alone (Seyfarth et al., 2012). In mountain gorillas, Sociability is associated with a higher rate of approaches to others, and Dominance and Proto-Agreeableness are positively and negatively associated, respectively, with rate of conflict intervention (Eckardt et al., 2015).

We know that humans show a wide degree of variation in their ability to perceive the emotions of others (Baron-Cohen & Wheelwright, 2004; Davis, 1980). We would expect to find similar variation in nonhuman primates. Furthermore, empathetic traits in humans have been associated with personality. Jolliffe & Farrington (2006) report positive correlations between cognitive empathy and measures of Extraversion, Agreeableness and Openness for both males and females, as well as a positive correlation of affective empathy and Agreeableness.

Personality is therefore an important consideration for future research assessing individual differences in social interactions and socio-emotional perception. This is particularly important in captivity, where individuals are limited in who they choose to socialise with. Differences in empathetic response may thus determine how individuals are affected by their conspecifics in a social environment (Edgar et al., 2012). By establishing whether personality relates to how individuals perceive each other, we may begin to understand more about links between personality, well-being and longevity, particularly if these are variables influenced by social environment (King & Landau, 2003; Weiss et al., 2009; Weiss et al., 2013).

In assessing emotional perception, individual differences can play an important role in aiding our understanding of this complex field. It will provide detail on how individuals cope and respond within a social group; and will benefit an understanding of emotional perception as a whole, by considering that displays of different levels of emotional perception – from contagion to perspective taking – may vary across individuals. This approach, which will assess behaviours displayed at different levels, allows us to examine (1) to what extent individuals differ in how they respond to emotions, and whether personality predicts differences in response. (2) Given the uncertainty of whether chimpanzees display cognitive empathy, we can explore whether chimpanzees demonstrate emotional perspective taking, and whether personality is associated with individual differences in perspective taking. (3) Finally, we can also examine to what extent different levels of emotional perception correlate with each other.

1.5 Linking Personality to Emotional and Social Perception, Social Interactions and Well-being

Taking a multi-species approach, in this thesis I integrate personality assessment with behavioural and experimental methods that assess the role of individual differences in three key areas: (1) well-being (2) social interactions and emotional perception, (3) facial morphology and face perception.

I start by examining personality at the species level, by comparing personality structure in two species of squirrel monkey, and its relation to subjective well-being (Chapter 2). This study is important for two reasons. Firstly, it contributes to the growing body of comparative primate personality research, in particular, expanding research for New World monkeys which to date, has remained somewhat limited compared to their Old World counterparts. Secondly, assessing well-being in these species helps not only to inform our understanding of why personality relates to well-being, but can put well-being in the context of social behaviour. Given the potential applications of differential research to improving well-being for captive animals, it is important to explore the inter-relation of well-being with personality and social behaviours.

Following on from this I introduce a study in which we used personality measures in captive chimpanzees to assess individual differences in autistic-like traits (Chapter 3), and their relation to social interactions (Chapter 4). Expanding from the discussion of well-being, this approach focuses on the need to better understand differential behaviour in captivity for the purposes of improving individual welfare.

The next study (Chapter 5) introduces the experimental work of this thesis with the assessment of emotional perception in chimpanzees. Whilst understanding empathetic behaviours also has consequences for welfare applications, this section leans towards a more methodological focus by examining the role of personality in predicting responses to emotions in conspecifics – both in a group setting, and using experimental video stimuli.

Whilst Chapter 5 considers personality as a predictor of response to others, in the next section I examine how individuals respond to others' personality traits. Considering the face as a potential signal of dominance-related traits, here I first explore the associations between personality and facial morphology (Chapter 6), and then assess whether individuals can perceive differences in facial morphology associated with variation in Assertiveness (Chapter 7).

Finally, I summarise these findings in Chapter 8 and discuss the goals and next steps for the differential approach to studying social behaviour.

Chapter 2. Personality and Well-being in Two Species of Squirrel Monkey

> *"A very small proportion of primate species are represented in the primate personality literature… [only 7%] have been studied in relation to personality."*
>
> \- Hani D. Freeman & Samuel D. Gosling (2010, p. 4)

2.1 The Diversity and Origins of Personality

Research into the personalities of nonhuman primates has expanded rapidly in the last two decades (Freeman & Gosling, 2010). One development that has benefitted personality research has been the use of standardised measurement instruments for assessing personality structure across members of taxonomic groups.

One such tool is the Hominoid Personality Questionnaire, widely used for assessing personality structure across primate taxa. Initially developed as the Chimpanzee Personality Questionnaire[5] (King & Figueredo, 1997) it has since been validated in multiple chimpanzee populations, and expanded into the current 54 item Hominoid Personality Questionnaire (HPQ) (King, Weiss & Farmer, 2005; Weiss et al., 2007; Weiss et al., 2009). It has further been used and validated in all nonhuman great ape species (Eckardt et al., 2015; Schaefer & Steklis, 2014; Weiss et al., 2006;

---

[5] Development of this questionnaire in chimpanzees shall be discussed in more detail in Chapter 3.

Weiss et al., 2015), as well as Old World monkeys, including hanuman langurs and six species of macaque (see Table 2.1) (Adams et al., 2015; Konečná et al., 2008; Konečná, Weiss, Lhota, & Wallner, 2012; Weiss et al., 2011). Recently, assessment using the HPQ was expanded to New World monkeys, with a study assessing personality in brown capuchins (Morton, Lee, Buchanan-Smith, et al., 2013).

Research using the HPQ and similar questionnaires (Eckardt et al., 2015; King & Figueredo, 1997; Weiss et al., 2006; Weiss et al., 2009) has shown that like humans (McCrae & Costa, 1985), chimpanzees (*Pan troglodytes*) (King & Figueredo, 1997; Weiss et al., 2009), and orangutans (*Pongo spp.*) (Weiss et al., 2006), possess a Neuroticism dimension, but bonobos (*Pan paniscus*) (Weiss et al., 2015) and mountain gorillas (*Gorilla beringei beringei*; Eckardt et al., 2015) do not. Evidence for a Neuroticism dimension in western lowland gorillas (*Gorilla gorilla gorilla*) is mixed. One study of eight males found no evidence (Schaefer & Steklis, 2014) but an earlier, larger study using a different questionnaire found evidence of a dimension ("Fearful") that resembled Neuroticism (Gold & Maple, 1994).

Table 2.1

Personality dimensions across species, determined using variants of the Hominoid Personality Questionnaire

Humans[1]	Chimps[2,3]	Bonobos[4]	E.M. gorillas[5]	W.L. gorillas[6]	Orangutans[7]	Macaques[8,9,10]	Hanuman Langurs[11]	Brown Capuchins[12]	Common Marmosets[13]
Opn	Opn	Opn	Opn	---	Int	Opn[R,J, B, A, T]	---	Opn	Opn
Con	Con	Con	---	Con	---	---	---	---	Con
---	---	Atn	---	---	---	---	---	Atn	
Ext	Ext	Ext	Soc	Ext/Agr	Ext	Soc[T]	Ext	Soc	Ext
Agr	Agr	Agr	Proto-Agr	---	Agr	Act[R, A, B]	Agr	---	Agr
---	---	---	---	---	---	Exc[C,B]	---	---	---
---	---	---	---	---	---	Frd[R,J, B, A, T,C]	---	---	---
---	---	---	---	---	---	Irr[B]	---	---	---
Neu	Neu	---	---	---	Neu	Anx[R,J]	---	Neu	---
---	---	---	---	---	---	Cnf[R,B, A,C]	Cnf	---	---
---	Dom	Ast	Dom	Dom	Dom	Dom[R,J, T]	---	Ast	---
---	---	---	---	---	---	Agg[C]	---	---	---
---	---	---	---	---	---	Opp[A,B]	---	---	---

Note. Left hand column indicates original FFM in humans. E.M. = Eastern Mountain; W. L. = Western Lowland; Opn = Openness; Int = Intellect; Con = Conscientiousness; Atn = Attentiveness; Ext = Extraversion; Soc = Sociability; Agr = Agreeableness; Proto-Agr = Proto-Agreeableness; Act = Activity; Frd = Friendliness; Irr = Irritability; Neu = Neuroticism; Anx = Anxiety; Cnf = Confidence; Dom = Dominance; Ast = Assertiveness; Agg = Aggressiveness; Exc = Excitability; Opp = Opportunism. --- = NA.

[1]McCrae & Costa (1987) [2]King & Figueredo (1997) (43 items); [3]Weiss et al. (2009); [4]Weiss et al. (2015); [5]Eckardt et al. (2014); [6]Schaefer & Stecklis (2014); [7]Weiss et al. (2006) (51 items); [8]Weiss et al. (2011); [9]Adams et al. (2015); [10]Konečná et al. (2012) (51 items); [11]Konečná et al. (2008) (51 items); [12]Morton, Lee, Buchanan-Smith, et al. (2013); [13]Iwanicki & Lehmann (2015) (47 items using a combination of 5 questionnaires including items from the CPQ[2]); non-denoted studies used 54 items. [R] = Rhesus; [J] = Japanese; [B] = Barbary; [A] = Assamese; [C] = Crested; [T] = Tonkean.

Recently, these measures enabled researchers to compare sex and age differences in personality across nonhuman primates. For example, age-related declines in Extraversion have been found both in social species, including humans (Donnellan & Lucas, 2008; Terracciano, McCrae, Brant, & Costa, 2005), chimpanzees (King, Weiss, & Sisco, 2008), and in semi-solitary orangutans (Weiss & King, 2015), suggesting that age-related declines in Extraversion have a long evolutionary history. In contrast, Agreeableness increases with age in chimpanzees (King et al., 2008) and humans (Donnellan & Lucas, 2008; Terracciano et al., 2005), but not in orangutans (Weiss & King, 2015), suggesting that stronger selection pressures for developmental increases in Agreeableness are present in social species (Weiss & King, 2015). Similar differences have been found when comparing sex differences in Agreeableness. Like humans (Soto, John, Gosling, & Potter, 2011) female chimpanzees are higher in Agreeableness than males, but there is no evidence for sex differences in this dimension among orangutans (Weiss & King, 2015). This again points to the possibility of group living as a selective pressure that influences personality.

Comparing the personality structures of Catarrhines, the taxonomic group that includes Old World monkeys and great apes, and Platyrrhines, the New World monkeys, as well as comparing Platyrrhine species would help further our knowledge about personality phylogeny. Currently, personality studies in New World monkeys are outnumbered almost 3 to 1 by assessments in Old World species (Freeman & Gosling, 2010). Specifically, these comparisons will enable us to explore the evolutionary origins of personality dimensions in Old World monkeys, great apes, and humans (Gosling & Graybeal, 2007). Finding similar personality dimensions in Catarrhines and Platyrrhines would suggest that those dimensions are ancestral and originated at some point prior to the divergence of these species approximately 43 million years ago (Steiper & Young, 2006) or that they evolved independently in both species. Finding different personality dimensions would indicate that, sometime after Catarrhines and Platyrrhines diverged, different selective pressures led to different sets of personality dimensions. In addition, comparing personality among Platyrrhines that differ in habitat or social structure enables us to determine what selective pressures might have contributed to the evolution of personality. For example, level of social tolerance - which is related to species differences in rank hierarchy - amongst macaque species is associated with species differences in traits relating to dominance and aggression (Adams et al., 2015). Following this, we expect that similar associations between socioecology and personality structure in Platyrrhines and Catarrhines would be strong evidence for similar selection pressures acting on personality structure.

To date, personality has been assessed in six New World monkey species, including cotton-top tamarins (Franks et al., 2013), common marmosets (Iwanicki & Lehmann, 2015; Koski & Burkart, 2015), white-faced capuchins (Manson & Perry, 2013), brown capuchins (Morton, Lee, Buchanan-Smith, et al., 2013; Uher, Addessi, & Visalberghi, 2013) and common and Bolivian squirrel monkeys (Martau, Caine, & Candland, 1985).

Although different methods were used to study personality in these species, patterns nevertheless emerge. For example, openness/exploratory behaviour has been observed in marmosets, capuchins and squirrel monkeys, as have behaviours relating to neurotic and sociable traits (Iwanicki & Lehmann, 2015; Koski & Burkart, 2015;

Manson & Perry, 2013; Martau et al., 1985; Morton, Lee, Buchanan-Smith, et al., 2013; Uher et al., 2013). Similarly, boldness has been observed in tamarins and marmosets (Franks et al., 2013; Koski & Burkart, 2015). These studies also found that these traits can be reliably measured (Manson & Perry, 2013; Martau et al., 1985; Morton, Lee, Buchanan-Smith, et al., 2013), are temporally stable (Manson & Perry, 2013a; Uher et al., 2013) and in the case of trait ratings, are associated with behaviours (Iwanicki & Lehmann, 2015; Morton, Lee, Buchanan-Smith, et al., 2013), social relationships (Morton, Lee, Buchanan-Smith, et al., 2013) and morphological measures (Lefevre et al., 2014; Wilson et al., 2014).

The use of similar and standardised measures allows us to directly compare species' personality. For example, assessment of brown capuchins using the HPQ found five dimensions (Morton, Lee, & Buchanan-Smith, 2013), four of which resembled the chimpanzee Dominance, Conscientiousness, Neuroticism, and Openness dimensions. A fifth dimension, Sociability, was made up of traits related to chimpanzee (and human) Extraversion and Agreeableness (Digman, 1990; King & Figueredo, 1997), which therefore resembled the rhesus macaque Friendliness dimension (Weiss et al., 2011). A study of common marmosets used a similar questionnaire, with traits derived from five questionnaires including the HPQ's precursor (Capitanio & Widaman, 2005; Freeman, 2010; King & Figueredo, 1997; Stevenson-Hinde & Zunz, 1978; Weiss, King, & Hopkins, 2007). Marmoset personality dimensions labelled Extraversion, Agreeableness, Openness and Conscientiousness were identified (Iwanicki & Lehmann, 2015). Dimensions resembling Conscientiousness (McCrae & Costa, 1985) have been found in chimpanzees (King & Figueredo, 1997), bonobos (Weiss et al., 2015), gorillas

(Schaefer & Steklis, 2014), and brown capuchins (Morton, Lee, Buchanan-Smith, et al., 2013), but not in macaques (Adams et al., 2015). These findings suggest that Conscientiousness evolved in New World monkeys via convergent evolution, and possibly is an adaptation for living in complex social groups (King & Weiss, 2011).

2.2 Comparative Assessment in Squirrel Monkeys

Expanding on previous work using the HPQ, in the first part of this study we compared two New World monkey species of the genus *Saimiri*, namely common (*S. sciureus*) and Bolivian (*S. boliviensis*) squirrel monkeys (see Figure 2.1). We also compared personality in these species to the previously assessed brown capuchin monkeys (*Sapajus apella*). As capuchins and squirrel monkeys are both of the Cebidae family (Harada et al., 1995), personality assessment of other species of Cebidae is a suitable next step for understanding the phylogeny of personality in New World monkeys.

Common and Bolivian squirrel monkeys diverged approximately 1.5 million years ago (Chiou, Pozzi, Lynch Alfaro, & Di Fiore, 2011), and *Saimiri* diverged from *Sapajus* between 16 and 19 million years ago (Opazo, Wildman, Prychitko, Johnson, & Goodman, 2006; Schneider & Sampaio, 2015). Common and Bolivian squirrel monkeys have different social structures (Boinski & Cropp, 1999; Boinski et al., 2002) and occupy different habitats (Boinski & Cropp, 1999; IUCN, 2015). Common squirrel monkeys are found in North-East Brazil, Colombia, French Guiana, Guyana, Suriname and Venezuela, while Bolivian squirrel monkeys' habitat covers a smaller range primarily to the west side of the amazon basin, including Bolivia, North-West Brazil and Peru.

Common squirrel monkeys live in small, male-dominated groups of 15-50 individuals and exhibit high levels of inter-male aggression. Due to patchy distribution of food resources in their habitat they also have high levels of within-group competition (Boinski & Cropp, 1999; Boinski et al., 2002). In addition, both males and females disperse from the natal group (Boinski, Kauffman, Ehmke, Schet, & Vreedzaam, 2005). Bolivian squirrel monkeys, on the other hand, live in groups of 45-75 individuals. These groups are female dominated and there are high levels of inter-female aggression, but less within-group competition for food resources than is found in common squirrel monkey groups (Boinski & Cropp, 1999; Boinski et al., 2002). Bolivian squirrel monkey females are philopatric and males disperse from their natal group at maturity (Boinski et al., 2005).

In addition to these differences, common squirrel monkeys share their habitat and form mixed species groups with brown capuchin monkeys (Fleagle, Mittermeier, & Skopec, 1981). This allows for further cross-species comparisons of personality. Brown capuchin monkeys live in groups of 10 to 40 individuals (Janson, Baldovino, & Di Bitetti, 2012). Females are philopatric and tend to form strong alliances, although alpha males are dominant over females (Di Bitetti, 1997). Brown capuchins and common squirrel monkeys thus share not just their habitat, but also have similar group sizes and male-dominated societies. On the other hand, unlike common squirrel monkeys, brown capuchins are socially tolerant and exhibit low levels of conflict (Izawa, 1980).

Moreover, like Bolivian squirrel monkeys, female capuchins are philopatric (Di Bitetti, 1997).

These species differences enable us to test several hypotheses. First, common squirrel monkeys and brown capuchins monkeys have overlapping habitats, similar group sizes, and male-dominated societies. Thus, if any of these factors influence personality, we would expect that brown capuchin personality should be more similar to common squirrel monkey personality than it is to Bolivian squirrel monkey personality. Second, Bolivian squirrel monkeys resemble brown capuchin monkeys but not common squirrel monkeys in that their societies are characterised by male dispersal and low in-group competition. If any of these factors influence personality evolution then we would expect that Bolivian squirrel monkeys should more closely resemble brown capuchin monkeys than they do common squirrel monkeys.

Figure 2.1

Common and Bolivian squirrel monkeys. Left: Common squirrel monkey, *Saimiri sciureus*, and right: Bolivian squirrel monkey, *Saimiri boliviensis*. Bolivian squirrel monkeys are distinguishable by the black cap on their heads, as well as more rounded arch of white hair above the eyes. Common squirrel monkeys tend to have a distinctly v-shaped arch above their eyes. Adult females also have short black sideburns, which are absent in males.

Thirdly, given that common squirrel monkeys experience higher resource competition than brown capuchins or Bolivian squirrel monkeys, we expect that traits related to aggression/competition will be higher in common squirrel monkeys than in Bolivian squirrel monkeys, and fourthly, that Bolivian squirrel monkeys and capuchins should be more similar in traits related to aggression/competition than Bolivian and common squirrel monkeys, or common squirrel monkeys and capuchins. Finally, if the personalities of both species of squirrel monkeys diverged little from that of the common ancestor of *Saimiri* then we expect that the two species of squirrel monkeys will have similar personalities to each other.

2.3 Personality and Well-being

In addition to understanding how personality traits diverged, personality assessment can be beneficial for captive management and welfare purposes (Gartner & Powell, 2012; Watters & Powell, 2012). In particular, personality is associated with individual differences in the ability to cope with physical and social environments. Understanding these associations can therefore enable people to better cater to the needs of individual animals. Meta-analyses of personality and subjective well-being in humans have found that high Neuroticism and low Extraversion are strong correlates of low well-being (DeNeve & Cooper, 1998; Steel et al., 2008). Similar associations have been found in chimpanzees and orang-utans, with well-being ratings correlating positively with Extraversion and Agreeableness, and negatively with Neuroticism, in both species (King & Landau, 2003a Weiss et al., 2009; Weiss et al., 2006). Well-being has also been associated with longevity in orang-utans, indicating that happier apes live longer (Weiss et al., 2011).

In great apes, as in humans, well-being shows a U-shaped curve across the lifespan (Weiss et al., 2012). Reflecting interspecific similarities in personality changes with age, these results suggest that well-being is not just found in humans but is ancestral, at least amongst the apes. Further evidence from rhesus macaques indicates similar links between personality and well-being - higher Confidence and Friendliness and lower Anxiety are associated with higher well-being ratings (Weiss, Adams, et al., 2011). Associations between similar personality dimensions and well-being have also been found in non-primate species, for example, in Scottish wild cats (Gartner & Weiss, 2013). From these findings, it is likely that we will find a similar construct of well-being in squirrel monkeys.

Both squirrel monkey species are abundant in captivity, and both are often used in behavioural research, making them a priority for well-being assessment from a welfare perspective. Thus, in addition to addressing personality, in the second part of this study we assessed well-being and its association with personality traits. The repeated observation that sociality and anxiety/fearfulness are associated with higher and lower well-being, respectively, suggests that the origins of these associations are deeply rooted within mammalian species. Finding similar associations in squirrel monkeys would support this hypothesis.

2.4 Methods for Personality Assessment

2.4.1 Subjects.

Common squirrel monkeys.

Personality ratings were collected for 63 monkeys from nine international zoos, primarily through email (see Table 2.2). All data were provided by zoo staff. All personality ratings for six monkeys from one location were excluded because all monkeys were scored as seven for the items sociable and solitary, indicating that care was not taken to provide accurate ratings. English language questionnaires were used to rate all of the samples except for a Czech sample, for which each item was verbally translated into Czech. The total sample included 33 males, 21 females, and nine monkeys for which sex was not provided. Age data were available for 44 monkeys, between 1 and 21 years old (mean age = 10.30 years, *SD* = 5.69 years). Where data were not provided, zoos were re-contacted and requested to provide missing information, but not all were able. Each monkey was rated by between one and four raters (mode = 3).

Bolivian squirrel monkeys.

Personality data were collected for 40 monkeys from six international zoos, primarily through email (see Table 2.2). All data were provided by zoo staff. English language questionnaires were used to rate all of the samples except a Japanese sample, which was rated using a Japanese translation of the HPQ (Weiss et al., 2009). The total sample included 14 males, 17 females, and nine monkeys for which sex was not provided. Age was available for 31 monkeys, between 1 and 17 years old (mean age = 8.32, *SD* = 5.21 years). Where data were not provided, zoos were re-contacted and requested to provide missing information, but not all were able. Each monkey was rated by between one and six raters (mode = 2).

Brown capuchin monkeys.

Personality ratings for 127 brown capuchins were collected previously as part of a study by Morton, Lee, Buchanan-Smith, et al., (2013). Data were collected from five different sites in the US, UK and France (see Morton, Lee, Buchanan-Smith, et al., (2013) for full details), and included 60 males and 67 females, with mean age of 11 years (SD = 8.9). Each monkey was rated by between one and seven raters. Component extraction revealed five personality dimensions, which were labelled Assertiveness, Openness, Neuroticism, Sociability and Attentiveness (see Morton, Lee, Buchanan-Smith, et al., (2013) for full details). For the present study we used item loadings of brown capuchins described by Morton and colleagues for comparisons with the squirrel monkey trait structures.

2.4.2 Instrument.

The HPQ consists of 54 items, each made up of an adjective followed by one to three sentences defining that adjective in the context of monkey behaviour (see Appendix B). For example, “FEARFUL: Subject reacts excessively to real or imagined threats by displaying behaviours such as screaming, grimacing, running away or other signs of anxiety or distress.” Keepers were asked to rate each animal on each item using a 7-point Likert scale where 1 indicates “Displays either total absence or negligible amounts of the trait” and 7 indicates “Displays extremely large amounts of the trait”. Raters were instructed to not discuss their ratings with each other.

Table 2.2

Descriptive statistics for information collected from each zoo

	Personality data						SWB data	
Zoo	Sample size	Males	Females	Rater mean	Mean months known	Mean age	Sample size	Rater mean
		Common squirrel monkeys						
Edinburgh Zoo, UK	21	6	15	2.9	12.21	6.2	---	---
Brights Zoo, USA	2	---	---	1	36	---	2	1
Exmoor Zoo, USA	3	2	1	1	36	---	2	1
Hellabrunn Zoo, Germany	4	2	2	2	86.25	8.7	4	2
Leipzig Zoo, Germany	6	---	---	2	---	---	6	2
Oakland Zoo, USA	3	2	1	2	61	18	---	---
Olomouc Zoo, CR	3	1	2	1	---	---	---	---
San Francisco Zoo, USA	18	18	0	1	30	13.8	---	---
Singapore Zoo, Singapore	3	2	---	2.3	69.33	---	3	2.3
Total	63	33	21				17	
		Bolivian squirrel monkeys						
Bellewaerde Park, Belgium	2	1	1	4.5	---	6.5	---	---
Dublin Zoo, Ireland	2	2	0	2	50	7	2	2
Japan Monkey Centre, Japan	21	8	13	5.4	19.27	9.1	21	5.4
Peaugres Zoo, France	9	---	---	1	---	---	9	1
Salzburg Zoo, Austria	2	1	1	2	37.5	10.5	2	2
Wellington Zoo, NZ	4	2	2	2	24.5	7	3	1.5
Total	40	14	17				37	

2.4.3 Analyses.

All analyses were run in R version 3.0.2 (R Core Team, 2013).

Item reliabilities.

For squirrel monkeys rated more than once, we examined the interrater reliability of items using intraclass correlation coefficients (Shrout & Fleiss, 1979). The reliability of individual ratings were estimated using *ICC*(3,1) and the reliability of mean ratings across *k* raters we estimated using *ICC*(3,*k*). We estimated interrater reliabilities for common and Bolivian squirrel monkeys, separately, and for the combined sample. Items with an *ICC*(3,1) less than or equal to zero were excluded from further analyses.

Species-level analyses.

For each species separately and for the combined sample – forming a genus-level analysis - we performed a principal components analysis (PCA) on the mean item ratings per monkey for all reliable items. We determined the number of components to extract using a parallel analysis and by inspecting the scree plot. We applied an oblique (promax) and orthogonal (varimax) rotation to the solution. If the promax rotation revealed high inter-factor correlations and a noticeably different structure, we interpreted the obliquely rotated components. If the inter-factor correlations were modest and the structures were similar, we interpreted the orthogonally rotated components.

We then, for each species and for the genus-level structure, created unit-weighted factor scores by summing items according to their highest, salient loading on each component. Any item with a negative loading was reversed. Salient loadings were defined as those that exceeded |0.4|. The unit-weighted scores were then standardised (mean = 0, *SD* = 1).

For zoos that housed a greater number of monkeys (two per species), we tested for between-zoo differences using an independent Welch two sample *t*-test in each species. As data were not normally distributed, we generated 95% confidence intervals using bias-corrected and accelerated bootstrapping for 500 samples.

To test for sex and age differences in the personality components of each species, we used linear models. One personality component was the dependent variable in each model. Sex, age and the sex x age interaction were the predictor variables. Due to skewness of the personality data, we determined the 95% confidence intervals for each model using bias-corrected and accelerated bootstrapping, for 500 samples.

Cross-species comparisons.

We used three approaches to compare the component structures of the squirrel monkeys and the brown capuchin monkeys (see Morton, Lee, Buchanan-Smith, et al., (2013) for full details of brown capuchin personality). First, for the PCA of the common squirrel monkey ratings and the PCA of the Bolivian squirrel monkey ratings, we indicated where each item loaded on the other squirrel monkey species and on brown capuchin monkeys. To determine whether common or Bolivian squirrel monkeys were more similar to capuchin monkeys we counted the number of items that squirrel monkey components shared with capuchin monkey components. Second, as in other studies (Weiss, Adams, et al., 2011), we computed unit-weighted component scores for each squirrel monkey species based on the trait structure of brown capuchins (for personality structure of brown capuchins, see Table A3 in Appendix A) and the trait structure of the other squirrel monkey species. We then ran bootstrapped Pearson's correlations between these scores and each species' own component scores. Third, we compared the component structures using three targeted orthogonal Procrustes rotations (McCrae, Zonderman, Costa, Bond, & Paunonen, 1996). The first targeted rotation compared the species-specific personality structures for Bolivian and common squirrel monkeys. For this analysis, we rotated the Bolivian squirrel monkey loadings (the smaller sample) toward the common squirrel monkeys loadings (the larger sample). We took the common squirrel monkey loadings as the target sample in this case due to their larger sample size, as a larger sample size is likely to give a more accurate estimate of the population component structure (McCrae et al., 1996). For the second rotation, we rotated the loadings of the common and Bolivian squirrel monkeys towards the genus-level loadings. For this analysis, we dropped 17 randomly selected subjects from the common squirrel monkeys so that both of the species-level structures were based on the same number of individuals. Finally, we tested for sex differences between the two species in the genus-level component scores using bootstrapped linear models, with personality component as the dependent variable and independent variables of species, sex, and species x sex interaction.

2.5 Methods for Well-being Assessment

2.5.1 Subjects.

Common squirrel monkeys.

Of the full sample, subjective well-being ratings were collected for 17 monkeys from five of the participating zoos (see Table 2.2). English language questionnaires were used to rate all of the samples. The total sample included five males, three females, and nine monkeys for which sex was not provided. Age data were available for five monkeys, between 3 and 15 years old (mean age = 9.4, *SD* = 4.93 years). Each monkey was rated by between one and three raters (mode = 2).

Bolivian squirrel monkeys.

Of the full sample, subjective well-being ratings were collected for 37 monkeys from five of the participating zoos (see Table 2.2). English language questionnaires were used to rate all of the samples except a Japanese sample, which was rated using a Japanese translation of the SWB questionnaire (Weiss et al., 2009). The total sample included 12 males, 16 females, and nine monkeys for which sex was not provided. Age data were available for 28 monkeys, between 1 and 17 years old (mean age = 8.39, *SD* = 5.45 years). Each monkey was rated by between one and six raters (mode = 2).

2.5.2 Instrument.

The Subjective Well-being Questionnaire (SWB) was designed based on human measures of well-being such as the Satisfaction With Life Scale (Pavot & Diener, 1993), to assess chimpanzee well-being (King & Landau, 2003) (see Appendix B). It consists of four items with a description of two to three sentences, for example, “Estimate the amount of time the monkey is happy, contented, enjoying itself, or otherwise in a positive mood. Assume that at other times the monkey is unhappy, bored, frightened, or otherwise in a negative mood”. Each item is rated on a 7-point Likert scale, where 1 indicates “Displays either total absence or negligible amounts of the trait” and 7 indicates “Displays extremely large amounts of the trait”. The first three items ask the rater to estimate the extent to which the monkey has positive mood, enjoys social interactions, and is successful in achieving its goals. The last item asks the rater how happy they would be if they were that monkey for a week. Raters were again asked not discuss their ratings with each other.

2.5.3 Item reliabilities.

For squirrel monkeys rated more than once, we examined the interrater reliability of items using intraclass correlation coefficients (Shrout & Fleiss, 1979). The reliability of individual ratings were estimated using *ICC*(3,1) and the reliability of mean ratings across *k* raters we estimated using *ICC*(3,*k*). We estimated interrater reliabilities for common and Bolivian squirrel monkeys, separately. Items with an *ICC*(3,1) less than or equal to zero were excluded from further analyses.

2.5.4 Well-being structure and relation to personality.

For Bolivian squirrel monkeys[6] we performed a principal components analysis (PCA) on the mean item ratings per monkey for all reliable SWB items. We determined the number of components to extract using a parallel analysis and by inspecting the scree plot. We applied an orthogonal (varimax) rotation to the solution.

We then created unit-weighted factor scores by summing items. Salient loadings were defined as those that exceeded |0.4|. The unit-weighted scores were then standardised (mean = 0, *SD* = 1).

For zoos that housed a greater number of monkeys, we tested for between-zoo differences using independent Welch two sample *t*-tests. As data were not normally distributed, we generated 95% confidence intervals using bias-corrected and accelerated bootstrapping for 500 samples.

---

[6] See Results for why we only did this for Bolivians and not commons

To test for a relationship with personality, we ran pearson's correlations, and calculated 95% confidence intervals for each correlation coefficient using bias-corrected and accelerated bootstrapping, for 500 samples.

2.6 Results for Personality Assessment

2.6.1 Species-level analyses

Interrater reliabilities.

We estimated interrater reliabilities for personality in 29 common squirrel monkeys. Items with an *ICC*(3,1) less than or equal to 0 included *irritable, inquisitive* and *unperceptive*. Reliable items for individual ratings ranged from < .01 for *conventional* to .58 for *autistic*. Reliable items for mean ratings ranged from .01 for *conventional* to .79 for *autistic* (see Table A1 in Appendix).

We estimated interrater reliabilities for personality items in 31 Bolivian squirrel monkeys. The only item with an *ICC*(3,1) less than or equal to 0 was *unperceptive*. The reliabilities of individual ratings ranged from .01 for *quitting* to .53 for *active*. The reliabilities of mean ratings ranged from .04 for *quitting* to .78 for *active* (see Table A1).

Personality structure.

We extracted components based on ratings of 57 common squirrel monkeys. The scree plot and parallel analysis indicated five components. However the fifth component, which contained loadings for six items---*manipulative, protective,* not *individualistic*---made little sense, so we extracted four components, which accounted for 58% of the variance. Promax rotation revealed that correlations between components did not exceed |.17|, thus we interpreted the varimax-rotated structure (Table 2.3).

Table 2.3

Item loadings on component structures for common squirrel monkeys

Common squirrel monkeys						Brown capuchins	Bolivian squirrel monkeys
Items	Opn	Neu	Ast	Agr	h^2	Loadings	Loadings
Impulsive	**0.83**	-0.10	-0.13	0.07	0.72	N	N
Excitable	**0.81**	-0.03	-0.05	0.02	0.66	N	N
Erratic	**0.78**	0.33	-0.08	-0.20	0.76	An-	N
Reckless	**0.77**	-0.18	0.24	-0.19	0.72	A	Ag-
Curious	**0.76**	-0.24	0.31	0.24	0.79	O	O-
Playful	**0.74**	-0.27	0.04	0.18	0.65	O	O-
Inventive	**0.71**	-0.10	0.15	0.30	0.63	O	O-
Predictable	**-0.70**	0.33	0.12	0.20	0.65	N-	N-
Active	**0.67**	**-0.47**	-0.14	0.27	0.76	O	O-
Defiant	**0.66**	0.18	0.02	0.11	0.48	N-	---
Jealous	**0.65**	0.18	0.19	**-0.51**	0.74	A	A
Stingy-Greedy	**0.65**	0.10	0.33	-0.14	0.56	A	A
Distractible	**0.63**	0.27	0.14	0.12	0.50	An-	O-
Innovative	**0.63**	-0.16	0.10	0.30	0.51	O	O-
Bullying	**0.62**	0.25	0.08	**-0.43**	0.63	A	A
Aggressive	**0.60**	0.07	0.33	-0.36	0.60	A	A
Imitative	**0.53**	0.25	-0.05	0.23	0.40	O	N
Cool	**-0.52**	0.39	0.22	0.21	0.52	N-	A
Manipulative	**0.51**	0.37	-0.12	-0.02	0.41	A	A
Solitary	-0.22	**0.81**	-0.18	-0.15	0.75	S-	O
Clumsy	0.12	**0.79**	-0.15	-0.08	0.67	An-	N

Items	Opn	Neu	Ast	Agr	h^2	Capuchin loadings	Bolivian loadings
Lazy	-0.17	**0.79**	0.13	-0.04	0.67	O-	O
Depressed	-0.11	**0.76**	**-0.40**	-0.07	0.75	A-	N
Conventional	-0.12	**0.66**	-0.08	0.10	0.47	O-	O
Autistic	0.23	**0.58**	-0.39	0.04	0.55	S-	N
Anxious	0.18	**0.58**	**-0.54**	-0.26	0.72	S-	N
Disorganised	0.22	**0.54**	-0.39	-0.24	0.55	An-	N
Unemotional	0.10	**0.52**	0.05	0.09	0.29	N-	O
Quitting	-0.04	**0.50**	-0.36	0.07	0.38	O-	N
Thoughtless	**0.44**	**0.45**	-0.04	-0.10	0.41	An-	N
Intelligent	0.03	0.38	0.33	0.31	0.35	---	N-
Independent	-0.10	0.02	**0.80**	-0.15	0.67	A	A
Dominant	0.23	-0.04	**0.77**	-0.34	0.76	A	A
Fearful	0.06	0.26	**-0.76**	-0.21	0.70	A-	N
Timid	-0.21	**0.42**	**-0.76**	-0.06	0.81	A-	N
Submissive	0.02	0.32	**-0.71**	**0.44**	0.80	A-	A-
Decisive	0.19	0.18	**0.70**	0.07	0.57	N-	N-
Vulnerable	0.22	0.33	**-0.62**	0.19	0.58	A-	N
Persistent	**0.42**	-0.03	**0.59**	-0.14	0.54	O	A
Cautious	-0.17	0.36	**-0.59**	-0.04	0.50	A-	N
Stable	0.07	0.24	**0.49**	0.24	0.36	N-	N-
Sociable	0.23	-0.18	**0.47**	0.40	0.47	S	Ag
Dependent-Follower	0.04	0.21	-0.34	0.05	0.17	A-	N
Friendly	0.19	-0.07	-0.22	**0.85**	0.81	S	Ag
Helpful	0.22	0.01	0.02	**0.79**	0.67	An	Ag
Sympathetic	-0.10	0.01	0.07	**0.78**	0.63	N-	Ag

Items	Opn	Neu	Ast	Agr	h^2	Capuchin loadings	Bolivian loadings
Gentle	-0.34	-0.04	-0.15	**0.77**	0.73	A-	Ag
Affectionate	0.27	-0.09	0.02	**0.74**	0.63	S	Ag
Sensitive	0.02	**0.47**	-0.15	**0.64**	0.65	---	Ag
Protective	-0.01	0.10	0.33	**0.46**	0.33	---	Ag
Individualistic	0.22	0.05	0.03	-0.23	0.10	---	A
Capuchin loadings*	O (7)	S-O-An	A (7)	S (2)			
Bolivian loadings*	O-A (6)	N (7)	N (6)	Ag (7)			

Note. Opn = Openness; Neu = Neuroticism; Ast = Assertiveness; Agr = Agreeableness; h^2 = Communalities. Letters in grey panel, and in bottom two rows, indicate item loadings on capuchin personality components (L) (Morton, Lee, Buchanan-Smith, et al., 2013) and Bolivian squirrel monkey components (R). Negative loadings indicated by "-". A = Assertiveness, O = Openness, N = Neuroticism, S = Sociability, An = Attentiveness, Ag = Agreeableness. NA indicated by "---".

*= Capuchin/Bolivian component with which each Common squirrel monkey component shows the highest congruence of item loadings (number of shared items in brackets).

Item loadings |>0.4| are highlighted in bold.

In the instance where items loaded on two components (for example *active, thoughtless*) we took the item to belong to the component on which it loaded the highest. Three items, *intelligent, dependent-follower* and *individualistic* did not have a salient loading on any component, suggesting they are weak items. Components were labelled based on the highest loading items on that component and its similarity with components found in other species. Labels included: Openness (not *predictable*, *excitable*, *impulsive*), Neuroticism (*anxious, depressed, solitary*), Assertiveness[7] (*dominant*, not *fearful,* not *timid*) and Agreeableness (*gentle, helpful, friendly*).

---

[7] We labelled this component Assertiveness, rather than Dominance, following Morton, Lee, Buchanan-Smith, et al. (2013).

We extracted components based on ratings for 40 Bolivian squirrel monkeys. The scree plot and the parallel analysis indicated that there were four components. Promax rotation revealed that correlation of components did not exceed |.23|, and so we again interpreted the results of a varimax rotation (see Table 2.4). Due to there being fewer subjects than items, the matrix eigenvalues were negative. To address this, eigenvalues were smoothed using the cor.smooth function (Revelle, 2015): this replaces each negative eigenvalue with 100*.Machine$double.eps (a numerical characteristic to the value of 2.220446e-16) , rescales them to sum to the number of items, then recomputes the matrix so that it is positive-definite. The components accounted for 63% of the variance. Two items, *defiant* and *individualistic* did not have a salient loading on any component. Components were labelled based on the highest loadings. We thus labelled the components Neuroticism (not *stable, timid, thoughtless*), Openness (*innovative, curious,* not *conventional*), Assertiveness (not *submissive, dominant, persistent*), and Agreeableness (*sympathetic, helpful, sensitive*).

Zoo differences.

We compared personality component scores between common squirrel monkeys at Edinburgh Zoo (n = 21) to common squirrel monkeys at San Francisco Zoo (n = 18). Neuroticism was significantly lower in the Edinburgh group (mean = -0.79) than in the San Francisco group (mean = 0.85), t(36.13) = -9.58, p < .001, 95% CI = [-13.13, -5.30]. There were no significant differences between zoos in Openness, t(21.17) = -1.67, p = .11, 95% CI = [-4.14, 0.47], Assertiveness, t(26.27) = 0.92, p = .37, 95 % CI = [-1.21, 3.10], or Agreeableness, t(28.38) = -1.32, p = .20, 95% CI = [-3.84, 1.03].

Table 2.4

Item loadings on component structures for Bolivian squirrel monkeys

	Bolivian squirrel monkeys					Brown capuchins	Common squirrel monkeys
Items	Neu	Opn	Ast	Agr	h^2	Loadings	Loadings
Thoughtless	**0.87**	-0.15	0.17	0.08	0.81	An-	N
Intelligent	**-0.81**	0.05	0.17	0.01	0.70	----	---
Anxious	**0.77**	0.36	-0.17	0.11	0.76	S-	N
Timid	**0.77**	0.39	-0.34	0.17	0.88	A-	A
Depressed	**0.76**	**0.43**	-0.12	0.06	0.78	A-	N
Disorganised	**0.75**	0.18	0.36	0.15	0.74	An-	N
Quitting	**0.73**	-0.15	0.12	0.35	0.70	O-	N
Clumsy	**0.73**	0.19	0.34	-0.06	0.69	An-	N
Cautious	**0.72**	0.29	-0.11	**0.43**	0.81	A-	A
Autistic	**0.72**	0.33	0.07	0.05	0.63	S-	N
Fearful	**0.72**	0.25	-0.18	-0.12	0.63	A-	A
Impulsive	**0.71**	-0.16	0.17	0.04	0.55	N	O
Excitable	**0.70**	-0.28	0.38	0.26	0.78	N	O
Vulnerable	**0.68**	**0.49**	-0.31	0.22	0.84	A-	A
Dependent-Follower	**0.66**	0.14	**-0.49**	0.25	0.76	A-	---
Imitative	**0.64**	-0.18	-0.09	**0.40**	0.61	O	O
Decisive	**-0.63**	-0.13	0.38	-0.17	0.59	N-	A-
Stable	**-0.62**	0.23	0.24	**0.41**	0.67	N-	A-
Predictable	**-0.58**	0.23	-0.07	-0.03	0.40	N-	O-
Irritable	**0.51**	-0.01	0.37	-0.28	0.48	A	---
Erratic	**0.45**	0.01	0.19	0.26	0.30	An-	O
Defiant	0.39	-0.38	0.25	0.26	0.42	N-	O
Lazy	0.36	**-0.76**	0.23	0.23	0.82	O-	N
Innovative	0.15	**0.75**	0.18	0.00	0.61	O	O
Curious	-0.16	**0.71**	**0.46**	-0.12	0.75	O	O
Active	-0.14	**0.70**	0.06	-0.22	0.56	O	O
Playful	-0.04	**0.69**	0.14	0.06	0.50	O	O
Conventional	-0.19	**-0.66**	0.12	0.26	0.55	O-	N
Inquisitive	0.23	**0.66**	**0.50**	-0.04	0.73	O	---
Inventive	-0.26	**0.63**	0.21	-0.13	0.52	O	O
Unemotional	0.36	**-0.61**	**0.40**	0.13	0.67	N-	N
Solitary	0.18	**-0.60**	0.21	-0.38	0.58	S-	N
Distractible	0.38	**0.57**	0.20	-0.14	0.53	An-	O
Individualistic	0.26	0.39	0.25	-0.05	0.28	---	---

Items	Neu	Opn	Ast	Agr	h^2	Capuchin loadings	Common loadings
Persistent	0.06	0.05	**0.78**	0.24	0.67	O	A-
Dominant	-0.01	-0.22	**0.74**	-0.09	0.60	A	A-
Independent	0.00	0.23	**0.71**	0.15	0.58	A	A-
Stingy-Greedy	0.06	-0.27	**0.65**	-0.35	0.63	A	O
Jealous	0.15	**-0.41**	**0.62**	-0.21	0.63	A	O
Manipulative	**0.54**	0.10	**0.58**	0.35	0.76	A	O
Aggressive	0.18	-0.36	**0.58**	-0.26	0.57	A	O
Bullying	-0.16	-0.20	**0.57**	-0.31	0.49	A	O
Cool	-0.31	0.32	**0.51**	0.16	0.49	N-	O-
Submissive	**0.44**	0.34	**-0.47**	0.10	0.54	A-	A
Sympathetic	0.12	0.11	-0.12	**0.87**	0.80	N-	Ag
Helpful	0.00	-0.02	-0.11	**0.79**	0.63	An	Ag
Sensitive	0.23	0.18	0.18	**0.78**	0.72	---	Ag
Reckless	-0.16	-0.31	0.33	**-0.67**	0.69	A	O
Gentle	0.22	**0.41**	-0.15	**0.67**	0.68	A-	Ag
Affectionate	**0.46**	0.15	-0.10	**0.67**	0.68	S	Ag
Protective	-0.03	0.03	**0.47**	**0.64**	0.64	---	Ag
Friendly	0.15	-0.07	-0.04	**0.60**	0.39	S	Ag
Sociable	-0.38	**-0.47**	0.32	**0.51**	0.73	S	A-
Capuchin loadings*	A (7)	O (8)	A (8)	S (3)			
Common loadings*	N (7)	O (6)	O (6)	Ag (7)			

Note. Opn = Openness; Neu = Neuroticism; Ast = Assertiveness; Agr = Agreeableness; h^2 = Communalities. Letters in grey panel, and in bottom two rows, indicate item loadings on capuchin personality components (L) (Morton, Lee, Buchanan-Smith, et al., 2013) and common squirrel monkey components (R). Negative loadings indicated by "-". A = Assertiveness, O = Openness, N = Neuroticism, S = Sociability, An = Attentiveness, Ag = Agreeableness. NA indicated by "---". *= Capuchin/common component with which each Bolivian squirrel monkey component shows the highest congruence of item loadings (number of shared items in brackets).

Item loadings | >0.4 | are highlighted in bold

We compared personality scores between Bolivian squirrel monkeys living in the Japan Monkey Center (n = 21) and Peaugres Zoo (n = 9). Neuroticism was significantly higher in the Japan group (mean = 0.57) than in the Peaugres group (mean = -1.53), $t(28) = 15.71, p < .001$, 95% CI = [10.31, 20.38]. Agreeableness was also significantly higher in the Japan group (mean = 0.31) than in the Peaugres group (mean = -1.08),

$t(13.75) = 4.95$, $p < .001$, 95% CI = [2.04, 7.77]. There were no significant differences between zoos in Openness, $t(13.67) = -20.01$, $p = .06$, 95% CI [-4.56, 0.17] or Assertiveness, $t(19.57) = 1.76$, $p = .09$, 95% CI [-0.55, 4.48].

Age and sex differences.

For common squirrel monkeys the linear models revealed a main effect of sex for Assertiveness, with males scoring higher than females (see Table 2.5). We found no age effect for Assertiveness, but we did find an age x sex interaction, with male Assertiveness increasing with age and female Assertiveness decreasing with age. As there was only one older female (> 20 years) but multiple older males, we excluded the older female and re-ran the analysis. The sex effects, $b = 1.89$, $p = .009$, 95% CI = [1.02, 3.17] and the age x sex interaction, $b = -0.19$, $p = .02$, 95% CI = [-0.31, -0.08] were still significant. No other effects of sex, age, or sex x age were significant.

For Bolivian squirrel monkeys, linear models revealed that Openness showed a marginally significant decrease with age. We also found a marginally significant sex effect for Agreeableness, with females scoring higher than males. No other effects of sex, age, or the sex x age interaction were significant (see Table 2.5).

Table 2.5

Age and sex effects on personality in common and Bolivian squirrel monkeys

		Common squirrel monkeys		
	b	l-95%, u-95% CI	*SE*	*p*
		Neuroticism		
Intercept	-1.05	-1.47, -0.8	0.33	.003
Sex	0.29	-0.31, 0.82	0.45	.52
Age	0.04	0.00, 0.12	0.04	.33
Sex x Age	0.05	-0.02, 0.12	0.04	.21
		Openness		
Intercept	0.36	-0.20, 0.96	0.40	.38
Sex	0.80	-0.12, 1.66	0.54	.15
Age	-0.09	-0.14, 0.01	0.04	.054
Sex x Age	0.00	-0.10, 0.10	0.05	.93
		Assertiveness		
Intercept	-0.45	-1.45, 0.20	0.45	.32
Sex	**1.55**	0.71, 2.66	0.60	**.014**
Age	0.04	-0.02, 0.18	0.05	.45
Sex x Age	**-0.13**	-0.27, -0.05	0.06	**.032**
		Agreeableness		
Intercept	-0.61	-1.28, 0.03	0.35	.090
Sex	0.02	-0.84, 1.07	0.47	.97
Age	0.06	-0.03, 0.12	0.04	.13
Sex x Age	-0.02	-0.09, 0.08	0.05	.69
		Bolivian squirrel monkeys		
	b	l-95%, u-95% CI	*SE*	*p*
		Neuroticism		
Intercept	0.77	0.03, 1.34	0.35	.035
Sex	0.04	-0.63, 0.88	0.43	.92
Age	-0.02	-0.08, 0.02	0.03	.44
Sex x Age	-0.06	-0.16, 0.04	0.05	.23

	b	l-95%, u-95% CI	*SE*	*p*
		Openness		
Intercept	0.43	-0.73, 1.41	0.49	.38
Sex	0.40	-0.79, 1.93	0.60	.51
Age	**-0.09**	-0.17, 0.00	0.04	**.044**
Sex x Age	0.02	-0.13, 0.16	0.06	.79
		Assertiveness		
Intercept	-0.93	-1.58, 0.01	0.59	.13
Sex	0.48	-0.59, 1.95	0.73	.52
Age	0.10	0.00, 0.16	0.05	.080
Sex x Age	0.01	-0.15, 0.18	0.08	.90
		Agreeableness		
Intercept	1.16	0.26, 2.15	0.48	.022
Sex	**-1.24**	-2.28, 0.29	0.59	**.044**
Age	-0.06	-0.13, 0.02	0.04	.20
Sex x Age	0.07	-0.20, 0.19	0.06	.30

Note. Bold cells indicate a significant effect for that variable.

2.6.2 Cross-species comparisons.

Personality structure.

Comparisons of the common squirrel monkey trait structure with the structures of brown capuchin and Bolivian squirrel monkeys revealed that Openness and Assertiveness shared the most trait loadings with capuchin Openness and Assertiveness, respectively. Common squirrel monkey Neuroticism and Agreeableness shared the most traits with Bolivian Neuroticism and Agreeableness, respectively (Table 2.3, grey panels).

Comparisons of the Bolivian squirrel monkey trait structure with the structures of brown capuchin and common squirrel monkeys revealed that Neuroticism shared traits equally with capuchin Assertiveness and common squirrel monkey Neuroticism. Bolivian squirrel monkey Openness and Assertiveness shared the most traits with capuchin Openness and Assertiveness, while Agreeableness shared the most traits with common squirrel monkey Agreeableness (Table 2.4, grey panels).

Table 2.6 displays the correlations between components defined by each squirrel monkey species' own component structure and those of the two other species. For comparisons between the two squirrel monkey species and brown capuchin monkeys, common squirrel monkey Neuroticism was most strongly, negatively correlated with brown capuchin Sociability and Attentiveness; Bolivian squirrel monkey Neuroticism showed the strongest, negative, relationship with brown capuchin Attentiveness, and a smaller positive correlation with Neuroticism. Openness for both squirrel monkey species was most strongly, positively correlated with brown capuchin Openness. Both common and Bolivian squirrel monkey Assertiveness was strongly positively correlated with brown capuchin monkey Assertiveness. Agreeableness showed the least similarity to brown capuchin monkey components; in common squirrel monkeys it correlated positively with Sociability and in Bolivian squirrel monkeys it correlated negatively with Assertiveness.

For comparisons between squirrel monkey components, common squirrel monkey Neuroticism was positively correlated with Bolivian squirrel monkey Neuroticism, and negatively correlated with Bolivian squirrel monkey Openness. Bolivian squirrel monkey Neuroticism correlated positively with common squirrel monkey Neuroticism, and negatively with Assertiveness. Common and Bolivian squirrel monkey Openness and Agreeableness, respectively, both showed the strongest, positive correlations with each other.

Common squirrel monkey Assertiveness correlated negatively with Bolivian squirrel monkey Neuroticism and positively with Bolivian Assertiveness. Bolivian squirrel monkey Assertiveness correlated positively with common squirrel monkey Openness and Assertiveness.

These correlations suggest that common and Bolivian squirrel monkeys are most similar in Neuroticism and Agreeableness, but that each squirrel monkey species are more similar to capuchins than to each other in Openness and Assertiveness. For Openness and Assertiveness, Bolivian squirrel monkeys share stronger correlations with brown capuchins than common squirrel monkeys do, suggesting that brown capuchin trait structure is more similar to that of Bolivian rather than common squirrel monkeys.

For our targeted orthogonal Procrustes rotations we first rotated the Bolivian squirrel monkey structure towards the common squirrel monkey structure. Congruence coefficients indicate similarity between items and components. Coefficients exceeding .85 are considered to indicate fair replicability, and coefficients exceeding .95 indicate good replicability (Lorenzo-Seva & Ten Berge, 2006). Eight items had congruence coefficients greater than .95, 19 items had congruence coefficients greater than .85, and 24 items had congruence coefficients less than or equal to .85 (see Table 2.7). All component level congruence coefficients were greater than .78. Congruence was highest for Assertiveness (.879). The overall congruence was .82 suggesting that the Bolivian squirrel monkey structure was not similar to the common squirrel monkey structure.

Table 2.6

Correlation coefficients between species personality-structure scores for squirrel monkeys and brown capuchins

	Neuroticism	Openness	Assertiveness	Agreeableness
Brown capuchins		Common squirrel monkeys [1]		
Neuroticism	-.16 [-0.38, 0.12]	**.58 [0.38, 0.71]**	-.24 [-0.53, 0.11]	**-.35 [-0.61, -0.09]**
Openness	**-.38 [-0.61, -0.09]**	**.78 [0.58, 0.88]**	**.36 [0.05, 0.62]**	.21 [-0.12, 0.47]
Assertiveness	-.23 [-0.52, 0.04]	**.61 [0.37, 0.75]**	**.81 [0.67, 0.91]**	**-.32 [-0.60, -0.05]**
Sociability	**-.83 [-0.88, -0.74]**	.13 [-0.24, 0.48]	**.50 [0.26, 0.68]**	**.37 [0.07, 0.61]**
Attentiveness	**-.74 [-0.80, -0.60]**	**-.54 [-0.73, -0.19]**	.19 [-0.09, 0.46]	.24 [-0.06, 0.48]
Brown capuchins		Bolivian squirrel monkeys [2]		
Neuroticism	**.63 [0.28, 0.73]**	.32 [-0.02, 0.53]	-.03 [-0.30, 0.25]	-.13 [-0.48, 0.12]
Openness	-.14 [-0.44, 0.20]	**.93 [0.88, 0.96]**	**.45 [0.13, 0.64]**	-.12 [-0.46, 0.21]
Assertiveness	**-.50 [-0.67, -0.17]**	**.50 [0.26, 0.66]**	**.84 [0.67, 0.92]**	**-.41 [-0.61, -0.13]**
Sociability	**-.60 [-0.73, -0.40]**	**.53 [0.31, 0.72]**	.11 [-0.29, 0.42]	.28 [-0.01, 0.54]
Attentiveness	**-.86 [-0.91, -0.72]**	.05 [-0.21, 0.33]	-.26 [-0.52, 0.02]	-.12 [-0.42, 0.40]
Bolivian squirrel monkeys		Common squirrel monkeys [3]		
Neuroticism	**.76 [0.61, 0.83]**	**.36 [0.04, 0.60]**	**-.70 [-0.80, -0.53]**	-.07 [-0.40, 0.25]
Openness	**-.51 [-0.71, -0.28]**	**.70 [0.52, 0.84]**	.31 [-0.02, 0.57]	.21 [-0.05, 0.55]
Assertiveness	-.01 [-0.34, 0.26]	**.60 [0.36, 0.77]**	**.69 [0.40, 0.83]**	**-.33 [-0.55, -0.03]**
Agreeableness	-.04 [-0.35, 0.29]	-.12 [-0.43, 0.28]	-.05 [-0.41, 0.27]	**.98 [0.97, 0.99]**
Common squirrel monkeys		Bolivian squirrel monkeys [4]		
Neuroticism	**.85 [0.76, 0.91]**	**-.54 [-0.72, -0.29]**	.07 [-0.25, 0.37]	.28 [-0.10, 0.59]
Openness	.26 [-0.14, 0.50]	**.70 [0.53, 0.80]**	**.66 [0.48, 0.78]**	-.09 [-0.40, 0.22]
Assertiveness	**-.75 [-0.83, -0.62]**	**.43 [0.14, 0.62]**	**.64 [0.40, 0.82]**	-.17 [-0.40, 0.09]
Agreeableness	.38 [-0.03, 0.61]	-.25 [-0.51, 0.07]	-.08 [-0.37, 0.19]	**.99 [0.98, 0.99]**

Note. Bootstrapped 95% CIs in brackets. [1]Common squirrel monkey scores are correlated with their scores using the definitions of brown capuchins. [2] Bolivian squirrel monkey scores are correlated with their scores using the definitions of brown capuchins. [3]Scores for common squirrel monkeys are correlated with their scores using the definitions of Bolivian squirrel monkeys. [4]Scores for Bolivian squirrel monkeys are correlated with their scores using the definitions of common squirrel monkeys. Significant correlations highlighted in bold.

To compare species-level structures with the genus-level structure, we first obtained the interrater reliabilities of the personality items in a combined sample of 60 common and Bolivian squirrel monkeys. The only item with an interrater reliability less than 0 was *unperceptive*. The reliabilities of individual ratings ranged from < .01 for *conventional* to .49 for *active*; the reliabilities of mean ratings ranged from < .01 for *conventional* to .74 for *active* (see Table A1). Next we conducted a PCA on the reliable items in a combined sample of 97 common and Bolivian squirrel monkeys. The scree plot and the parallel analysis indicated that there were five components. Promax rotation revealed that correlation of components did not exceed |.30|, and was similar in structure to the varimax rotation. Following Morton, Lee, Buchanan-Smith, et al. (2013), we interprated the correlations between these components as sufficiently low (< .45); we therefore interpreted the varimax rotation of these components, which accounted for 62% of the variance.

One item, *individualistic*, did not have a salient loading on any component, consistent with the independent personality structures in both species. We labelled the components Neuroticism (*depressed, anxious, clumsy*), Openness (*innovative, active, inquisitive*), Assertiveness (*aggressive, dominant, jealous*), Agreeableness (*sympathetic, friendly, affectionate*) and Decisiveness (*intelligent, decisive, independent*), again based on the highest loading items (see Table 2.8). Our next step was to extract five components for the common and Bolivian squirrel monkeys, separately, and to rotate these structures towards the genus-level structure. Rotation of the common squirrel monkey structure onto the genus-level structure revealed that four out of five components had congruence coefficients that exceeded .85 (see Table 2.9). Of the items, 23 had congruence greater than .95, 20 had congruence greater than .85, and 7 had congruence that were less than or equal to .85. The overall congruence was .914. Rotation of the Bolivian squirrel monkey structure towards the genus-level structure revealed that two out of five components had congruence coefficients exceeding .85 (see Table 2.10).

Table 2.7

Procrustes rotation: Solution matrix (Bolivians) is rotated onto the target matrix (commons)

Bolivian squirrel monkeys to common squirrel monkeys					
Item	Opn	Neu	Ast	Agr	Congruence
Aggressive	0.63	0.07	-0.30	-0.31	***.997***
Sociable	0.30	-0.24	-0.54	0.54	***.996***
Autistic	0.19	0.62	0.46	-0.07	***.984***
Sensitive	0.10	0.50	0.00	0.67	***.981***
Fearful	0.11	0.41	0.64	-0.19	***.972***
Timid	-0.03	0.52	0.78	0.09	***.966***
Defiant	0.61	0.09	0.06	0.25	***.959***
Lazy	-0.25	0.88	0.10	0.04	***.955***
Helpful	-0.02	0.08	0.04	0.82	*.948*
Playful	0.54	-0.40	-0.16	0.10	*.942*
Jealous	0.65	0.06	-0.35	-0.29	*.941*
Friendly	0.10	0.15	0.10	0.56	*.941*
Depressed	0.02	0.63	0.63	-0.06	*.939*
Dependent-Follower	0.03	0.23	0.80	0.26	*.938*
Anxious	0.06	0.57	0.66	0.00	*.937*
Unemotional	-0.07	0.83	-0.03	-0.08	*.931*
Sympathetic	-0.05	0.27	0.14	0.84	*.923*
Stingy-Greedy	0.52	0.10	-0.42	-0.43	*.916*
Protective	0.20	0.38	-0.39	0.56	*.912*
Disorganised	0.43	0.69	0.26	0.01	*.906*
Clumsy	0.39	0.64	0.27	-0.20	*.899*
Innovative	0.68	-0.34	-0.05	0.05	*.898*
Curious	0.62	-0.35	-0.46	-0.10	*.891*

Item	Opn	Neu	Ast	Agr	Congruence
Manipulative	0.50	0.69	-0.06	0.20	*.890*
Vulnerable	-0.13	0.57	0.70	0.12	*.885*
Excitable	0.76	0.39	0.19	0.17	*.858*
Thoughtless	0.64	0.42	0.46	0.00	*.851*
Dominant	0.51	0.18	-0.55	-0.16	.848
Submissive	-0.24	0.25	0.65	0.07	.848
Solitary	-0.26	0.52	0.01	-0.51	.829
Cautious	0.14	0.60	0.57	0.33	.809
Imitative	0.43	0.24	0.48	0.35	.804
Stable	-0.38	0.07	-0.61	0.39	.779
Active	0.43	-0.58	-0.16	-0.11	.779
Gentle	-0.23	0.47	0.25	0.58	.772
Impulsive	0.56	0.31	0.36	0.00	.769
Decisive	-0.08	-0.25	-0.71	-0.15	.745
Cool	-0.16	0.35	-0.58	0.08	.734
Conventional	-0.52	0.48	-0.20	0.16	.731
Erratic	0.32	0.36	0.16	0.22	.711
Distractible	0.68	-0.12	0.10	-0.15	.710
Persistent	0.36	0.510	-0.53	0.08	.709
Bullying	0.32	-0.02	-0.52	-0.33	.683
Predictable	-0.51	-0.15	-0.34	-0.02	.681
Affectionate	0.11	0.42	0.36	0.60	.654
Reckless	0.27	-0.27	-0.33	-0.66	.649
Independent	0.16	0.52	-0.51	0.03	.649
Inventive	0.39	-0.48	-0.34	-0.06	.642
Quitting	0.56	0.39	0.40	0.27	.637
Individualistic	-0.01	0.50	0.02	-0.16	.351
Intelligent	-0.39	-0.29	-0.68	0.07	.270
Overall	0.841	0.783	0.879	0.790	.820

Note. Opn = Openness; Neu = Neuroticism; Assertiveness; Agr = Agreeableness. Cells in bold italics indicate loadings > 0.95; cells in italics indicate loadings > 0.85.

Table 2.8

Item loadings on component structure for genus-level analysis of *Saimiri*

Items	Neu	Opn	Ast	Agr	Dec	h^2
Depressed	**0.86**	-0.17	-0.08	-0.01	-0.04	0.78
Anxious	**0.85**	0.05	-0.04	-0.15	-0.15	0.77
Clumsy	**0.79**	0.02	0.21	-0.02	0.13	0.68
Disorganised	**0.79**	0.18	0.08	-0.12	0.03	0.67
Timid	**0.76**	-0.19	-0.27	0.01	**-0.40**	0.85
Vulnerable	**0.72**	0.04	-0.18	0.16	-0.32	0.68
Autistic	**0.70**	0.02	0.09	0.10	-0.17	0.54
Lazy	**0.65**	-0.38	0.18	0.14	0.30	0.71
Cautious	**0.65**	-0.21	-0.07	0.16	-0.39	0.65
Solitary	**0.64**	-0.34	0.02	-0.18	0.30	0.64
Fearful	**0.62**	-0.03	-0.12	-0.18	**-0.46**	0.65
Thoughtless	**0.61**	0.39	0.20	-0.01	-0.03	0.56
Quitting	**0.60**	-0.04	0.13	0.21	-0.20	0.46
Submissive	**0.59**	0.00	-0.39	0.25	-0.29	0.64
Unemotional	**0.41**	-0.31	**0.41**	0.32	0.02	0.53
Individualistic	0.37	0.27	-0.04	-0.29	0.31	0.39
Innovative	0.09	**0.76**	0.06	0.02	0.13	0.61
Inventive	-0.10	**0.76**	0.12	0.03	0.22	0.65
Active	-0.30	**0.76**	0.00	0.04	-0.17	0.69
Inquisitive	-0.02	**0.75**	0.29	0.27	0.15	0.74
Curious	-0.29	**0.74**	0.32	0.09	0.18	0.78
Impulsive	0.35	**0.69**	0.22	0.02	-0.18	0.67
Playful	-0.28	**0.62**	0.20	0.18	-0.17	0.56
Excitable	0.38	**0.60**	0.35	0.10	-0.16	0.67
Distractible	0.24	**0.59**	0.29	0.08	0.09	0.50
Reckless	-0.25	**0.54**	**0.41**	-0.25	0.05	0.58
Erratic	**0.50**	**0.50**	0.36	-0.09	0.01	0.64
Conventional	0.32	**-0.47**	0.17	0.29	0.11	0.44
Defiant	0.20	**0.43**	**0.40**	0.21	-0.15	0.45
Aggressive	-0.02	0.23	**0.82**	-0.16	-0.11	0.77
Dominant	-0.21	0.07	**0.74**	-0.13	0.25	0.68

Items	Neu	Opn	Ast	Agr	Dec	h^2
Jealous	0.13	0.35	**0.70**	-0.27	0.01	0.70
Bullying	0.05	0.19	**0.69**	-0.26	0.02	0.58
Persistent	-0.03	0.18	**0.64**	0.11	0.27	0.52
Stingy-Greedy	-0.02	0.38	**0.62**	-0.08	0.13	0.56
Manipulative	**0.48**	0.10	**0.55**	0.27	-0.12	0.63
Irritable	0.39	0.37	**0.52**	-0.14	-0.03	0.58
Sympathetic	-0.03	-0.03	-0.23	**0.79**	0.05	0.69
Friendly	0.02	0.26	-0.24	**0.75**	-0.10	0.70
Affectionate	0.06	0.12	-0.05	**0.74**	-0.25	0.62
Helpful	-0.04	0.22	-0.21	**0.73**	0.05	0.63
Gentle	0.12	-0.15	**-0.44**	**0.68**	0.03	0.69
Sensitive	0.41	0.06	-0.18	**0.64**	0.22	0.66
Protective	-0.12	-0.12	0.28	**0.62**	0.15	0.51
Sociable	**-0.54**	0.08	0.33	**0.56**	0.03	0.72
Imitative	0.26	0.18	0.26	**0.46**	**-0.43**	0.56
Intelligent	-0.14	0.09	-0.14	0.08	**0.71**	0.56
Decisive	-0.30	0.19	0.15	-0.01	**0.69**	0.63
Independent	0.03	0.03	0.30	-0.08	**0.65**	0.52
Predictable	0.06	**-0.41**	-0.39	0.01	**0.55**	0.63
Cool	0.03	**-0.41**	0.02	0.23	**0.47**	0.45
Dependent-Follower	0.34	-0.06	-0.20	0.19	**-0.45**	0.40
Stable	-0.17	-0.14	0.24	0.36	**0.42**	0.42

Note. Neu = Neuroticism; Opn = Openness; Ast = Assertiveness; Agr = Agreeableness; h^2 = Communalities.

Item loadings | >0.4 | are highlighted in bold.

Table 2.9

Procrustes rotation: Solution matrix (commons) is rotated onto the *Saimiri* structure

	Common squirrel monkey to genus-level analysis					
Item	Neu	Opn	Ast	Agr	Dec	Congruence
Sociable	-0.44	0.11	0.36	0.51	0.09	***.990***
Friendly	-0.05	0.21	-0.14	0.90	-0.11	***.990***
Timid	0.74	-0.31	-0.29	-0.05	-0.25	***.979***
Curious	-0.36	0.71	0.25	0.23	0.20	***.977***
Vulnerable	0.62	0.04	-0.08	0.14	-0.42	***.976***
Cool	0.18	-0.55	0.09	0.35	0.59	***.975***
Solitary	0.74	-0.35	-0.09	-0.16	0.16	***.972***
Sensitive	0.36	0.17	-0.23	0.64	0.23	***.971***
Protective	-0.21	-0.21	0.36	0.51	0.12	***.970***
Distractible	0.34	0.71	0.28	0.19	-0.04	***.966***
Helpful	-0.10	0.26	-0.28	0.72	0.26	***.966***
Aggressive	-0.12	0.03	0.84	-0.22	-0.19	***.966***
Jealous	0.21	0.27	0.64	-0.42	-0.12	***.965***
Fearful	0.68	-0.12	-0.16	-0.14	-0.28	***.963***
Autistic	0.76	0.04	0.06	-0.03	-0.02	***.963***
Reckless	-0.14	0.65	0.48	-0.08	0.01	***.962***
Impulsive	0.20	0.79	0.29	0.11	-0.27	***.962***
Playful	-0.22	0.71	0.19	0.08	0.01	***.959***
Manipulative	0.41	-0.08	0.55	0.36	-0.27	***.958***
Predictable	0.11	-0.42	-0.55	0.08	0.41	***.957***
Decisive	-0.09	0.17	0.13	0.03	0.87	***.956***
Anxious	0.82	-0.11	-0.02	-0.32	0.00	***.955***
Active	-0.36	0.71	0.14	0.27	-0.06	***.954***
Inventive	-0.07	0.71	0.24	0.27	0.13	***.950***
Disorganised	0.80	0.04	-0.11	-0.18	0.20	*.948*
Depressed	0.81	-0.40	-0.16	-0.17	0.10	*.945*
Dominant	-0.47	-0.01	0.65	-0.23	0.37	*.937*
Sympathetic	-0.18	0.12	-0.26	0.66	0.15	*.937*
Erratic	0.56	0.37	0.53	0.08	-0.16	*.935*
Excitable	0.26	0.78	0.18	0.09	-0.15	*.930*
Submissive	0.58	0.05	-0.20	0.40	-0.54	*.926*
Imitative	0.33	0.18	0.36	0.53	-0.18	*.926*
Quitting	0.46	-0.16	0.13	0.11	-0.42	*.913*
Thoughtless	0.66	0.39	0.10	-0.10	0.31	*.906*
Lazy	0.76	-0.19	0.12	0.14	0.05	*.905*

Item	Neu	Opn	Ast	Agr	Dec	Congruence
Clumsy	0.71	-0.35	0.21	-0.01	0.34	*.893*
Bullying	0.29	0.16	0.75	-0.13	-0.27	*.888*
Individualistic	0.13	0.38	-0.10	-0.28	0.54	*.886*
Stingy-Greedy	0.11	0.57	0.42	-0.12	0.02	*.882*
Unemotional	0.32	-0.25	0.41	0.22	-0.37	*.870*
Cautious	0.52	-0.31	-0.13	-0.12	-0.15	*.868*
Independent	-0.33	-0.02	0.14	-0.21	0.75	*.867*
Intelligent	0.27	0.07	-0.20	0.22	0.73	*.857*
Innovative	-0.08	0.68	0.13	0.44	0.15	*.853*
Affectionate	-0.23	0.31	-0.07	0.71	0.04	.843
Gentle	-0.25	0.16	-0.43	0.68	0.00	.831
Conventional	0.58	-0.26	0.35	0.32	-0.17	.793
Persistent	-0.42	0.02	0.48	-0.03	0.45	.779
Defiant	0.22	0.07	0.52	0.46	0.05	.773
Stable	0.05	0.24	0.51	0.45	0.03	.521
Dependent-Follower	0.42	-0.14	-0.08	-0.11	0.05	.426
Overall	0.929	0.911	0.953	0.925	0.823	.914

Note. Neu = Neuroticism; Opn = Openness; Ast = Assertiveness; Agr = Agreeableness; Dec = Decisiveness. Cells in bold italics indicate loadings > 0.95; cells in italics indicate loadings > 0.85.

Of the items, 13 had congruence greater than .95, 25 had congruence greater than .85, and 15 had congruence that were less than or equal to .85. The overall congruence was .86. Based on these findings we concluded that common squirrel monkey personality was most similar to the genus-level.

Species differences.

Common squirrel monkeys scored significantly lower than Bolivian squirrel monkeys on Agreeableness (see Table 2.11 and Table 2.13). There were no other significant species differences in mean component scores. There were also no main effects of sex. However, we did find several interaction effects (see Table 2.12 and Table 2.13). Common squirrel monkey males, and Bolivian squirrel monkey females, were highest in both Neuroticism and Decisiveness.

Table 2.10

Procrustes rotation: Solution matrix (Bolivians) is rotated onto the *Saimiri* structure

	Bolivian squirrel monkey to genus-level analysis					
Item	Neu	Opn	Ast	Agr	Dec	Congruence
Dependent-Follower	0.51	-0.08	-0.26	0.18	-0.65	***.994***
Autistic	0.76	-0.04	0.10	0.02	-0.20	***.991***
Timid	0.79	-0.13	-0.25	0.11	-0.41	***.991***
Curious	-0.36	0.70	0.33	-0.03	0.26	***.982***
Lazy	0.74	-0.43	0.05	0.21	0.27	***.982***
Fearful	0.70	0.01	-0.10	-0.16	-0.32	***.978***
Depressed	0.88	-0.05	-0.18	0.03	-0.16	***.976***
Dominant	-0.09	0.17	0.78	-0.03	0.18	***.970***
Manipulative	0.56	0.12	0.54	0.38	0.05	***.970***
Inquisitive	0.02	0.81	0.35	0.05	0.16	***.965***
Protective	-0.01	-0.13	0.49	0.66	0.07	***.959***
Cautious	0.72	-0.10	-0.02	0.39	-0.38	***.958***
Vulnerable	0.79	-0.20	-0.30	0.16	-0.28	***.954***
Solitary	0.51	-0.29	0.02	-0.39	0.36	*.947*
Clumsy	0.74	0.12	0.34	-0.06	-0.09	*.941*
Sociable	-0.48	0.29	0.23	0.57	0.20	*.940*
Submissive	0.52	-0.13	-0.49	0.05	-0.22	*.940*
Excitable	0.47	0.44	0.46	0.29	-0.28	*.938*
Sensitive	0.35	-0.04	0.03	0.78	0.10	*.937*
Anxious	0.8	-0.06	-0.13	0.07	-0.31	*.937*
Thoughtless	0.67	0.41	0.25	0.10	-0.34	*.934*
Sympathetic	0.14	-0.16	-0.10	0.84	-0.18	*.925*
Friendly	0.20	0.23	-0.26	0.62	0.12	*.925*
Gentle	0.44	-0.24	-0.3	0.64	0.04	*.910*
Distractible	0.17	0.79	0.07	-0.07	0.03	*.908*
Bullying	-0.25	0.08	0.66	-0.27	0.14	*.902*
Stable	-0.31	-0.29	-0.04	0.44	0.59	*.899*
Cool	0.00	-0.25	0.27	0.20	0.57	*.893*
Innovative	-0.17	0.75	0.17	0.07	-0.10	*.891*
Active	-0.47	0.52	0.17	-0.18	-0.14	*.876*
Conventional	0.19	-0.58	-0.05	0.24	0.36	*.863*
Quitting	0.53	0.31	0.23	0.35	-0.39	*.859*
Stingy-Greedy	0.07	0.48	0.44	-0.26	0.44	*.857*
Affectionate	0.42	-0.09	-0.01	0.63	-0.33	*.854*
Defiant	0.06	0.25	0.53	0.27	-0.45	*.854*
Aggressive	0.05	0.47	0.54	-0.19	0.16	*.852*
Irritable	0.35	0.06	0.60	-0.28	-0.28	*.852*
Decisive	-0.54	-0.03	0.26	-0.12	0.46	*.852*

Item	Neu	Opn	Ast	Agr	Dec	Congruence
Persistent	0.24	0.17	0.50	0.31	0.54	.848
Predictable	-0.31	-0.27	-0.29	-0.03	0.46	.846
Disorganised	0.73	0.09	0.40	0.15	-0.16	.839
Playful	-0.22	0.77	-0.06	0.14	0.18	.830
Reckless	-0.18	0.42	0.17	-0.61	0.37	.773
Jealous	0.10	0.65	0.39	-0.12	0.39	.754
Helpful	-0.09	-0.18	0.03	0.76	-0.29	.741
Inventive	-0.51	0.44	0.26	-0.08	0.01	.716
Impulsive	0.43	0.22	0.44	0.03	-0.51	.715
Unemotional	0.74	-0.17	0.09	0.14	0.47	.678
Imitative	0.54	0.46	-0.2	0.42	-0.18	.666
Independent	0.14	-0.2	0.67	0.18	0.29	.653
Erratic	0.32	0.00	0.36	0.25	-0.31	.527
Intelligent	-0.70	-0.39	0.18	0.02	0.30	.384
Individualistic	0.35	-0.33	0.36	-0.08	-0.06	.093
Overall	0.927	0.826	0.847	0.905	0.730	.860

Note. Neu = Neuroticism; Opn = Openness; Ast = Assertiveness; Agr = Agreeableness; Dec = Decisiveness. Cells in bold italics indicate loadings > 0.95; cells in italics indicate loadings > 0.85.

Table 2.11

Mean genus-level component *z*-scores for common and Bolivian squirrel monkeys

	Neu	Opn	Ast	Agr	Dec
		Common squirrel monkeys			
Mean (*SD*)	0.25 (0.93)	0.18 (1.08)	0.16 (1.01)	-0.21 (1.00)	0.05 (0.97)
		Bolivian squirrel monkeys			
Mean (*SD*)	-0.35 (1.00)	-0.26 (0.81)	-0.22 (0.95)	**0.30 (0.93)**	-0.07 (1.05)

Note. Neu = Neuroticism; Opn = Openness; Ast = Assertiveness; Agr = Agreeableness; Dec = Decisiveness.

Bold score indicates that mean score is significantly higher in that species.

Table 2.12

Mean genus-level component *z*-scores by sex for common and Bolivian squirrel monkeys

	Neu	Opn	Ast	Agr	Dec
		Common squirrel monkeys			
Male M (*SD*)	0.44(0.99)	0.38 (1.18)	0.28 (0.95)	-0.18 (0.97)	0.22 (0.95)
Female M (*SD*)	-0.12(0.77)	-0.13 (0.85)	-0.25 (0.94)	-0.25 (1.11)	-0.27 (0.84)
		Bolivian squirrel monkeys			
Male M (*SD*)	-0.23 (0.69)	0.07 (0.88)	0.02 (1.17)	0.36 (0.72)	-0.57 (1.34)
Female M (*SD*)	0.30 (0.64)	-0.42 (0.59)	-0.11 (0.70)	0.85 (0.66)	-0.11 (0.72)

Note. Neu = Neuroticism; Opn = Openness; Ast = Assertiveness; Agr = Agreeableness; Dec = Decisiveness. M = mean.

2.7 Results for Well-being Assessment

2.7.1 Interrater reliabilities.

We estimated interrater reliabilities for well-being in 13 common squirrel monkeys which were rated by more than one rater. Items with an *ICC*(3,1) less than or equal to 0 included *goals* and *be monkey*.

We examined interrater reliabilities for well-being items in 26 Bolivian squirrel monkeys which were rated more than once. All items were reliable. ICCs for all well-being items are displayed in Table A1.

2.7.2 Well-being structure.

We had well-being ratings for a total of 17 common squirrel monkeys (including four rated only once). As only two items were reliable, we did not attempt component extraction for these two items. In the absence of a component structure, we summed mean ratings for the reliable well-being items (*mood* and *be social*) per monkey, and treated this as their well-being score.

Table 2.13

Genus-level personality components with species and sex effects

	b	l-95%, u-95% CI	*SE*	*P*
		Neuroticism		
Intercept	0.31	0.00, 0.63	0.20	.13
Species	-0.43	-1.00, -0.06	0.27	.12
Sex	-0.54	-0.88, 0.10	0.30	.077
Species x sex	**1.10**	0.38, 1.78	0.38	**.005**
		Openness		
Intercept	-0.42	-0.71, -0.14	0.23	.079
Species	0.28	-0.07, 0.95	0.31	.38
Sex	0.49	-0.31, 0.69	0.35	.16
Species x sex	0.02	-0.68, 0.84	0.44	.96
		Assertiveness		
Intercept	-0.11	-0.50, 0.20	0.23	.64
Species	-0.14	-0.58, 0.79	0.31	.64
Sex	0.12	-0.62, 0.47	0.34	.72
Species x sex	0.41	-0.43, 1.24	0.43	.35
		Agreeableness		
Intercept	0.83	0.54, 1.16	0.22	< .001
Species	**-1.06**	-1.01, -0.07	0.30	**< .001**
Sex	-0.49	-1.62, -0.41	0.33	.14
Species x sex	0.54	-0.27, 1.23	0.42	.20
		Decisiveness		
Intercept	-0.11	-0.45, 0.21	0.23	.63
Species	-0.15	-1.24, 0.28	0.31	.63
Sex	-0.46	-0.56, 0.39	0.35	.19
Species x sex	**0.95**	0.12, 1.89	0.44	**.033**

Note. Bold cells indicate a significant or close to significant effect for that variable.

For the Bolivian squirrel monkeys we ran component extraction for all four items based on ratings for a total of 37 monkeys (including eight monkeys rated only once). Examination of the scree plot and the parallel analysis indicated there was one component that accounted for 72% of the variance (see Table A2).

We examined between-zoo differences for Bolivian squirrel monkeys only, due to the larger sample size. Well-being was significantly lower in Japan (mean = -0.21) than in Peaugres (mean = 0.76), $t(22.96) = -3.67$, $p = .001$, 95 % CI [-7.08, -0.30].

2.7.3 Well-being correlations with personality.

We examined correlations between personality and well-being scores for a subset of 11 common squirrel monkeys with complete data. Due to the small sample size there were no p values < .05. However well-being was most strongly, positively, associated with Assertiveness (see Table 2.14).

For Bolivian squirrel monkeys (n = 37), we found that well-being was negatively and positively correlated with Neuroticism and Openness, respectively.

Table 2.14

Correlation coefficients and bootstrapped confidence intervals for personality and well-being components in common and Bolivian squirrel monkeys

	Neuroticism	Openness	Assertiveness	Agreeableness
	Common squirrel monkey (*n* = 11)			
SWB^1	-.28 [-0.79, 0.59]	-.17 [-0.72, 0.73]	.46 [-0.54, 0.84]	-.21 [-0.75, 0.65]
	Bolivian squirrel monkey (*n* = 37)			
SWB^2	**-.64 [-0.76, -0.41]**	**.47 [0.24, 0.67]**	.35 [-0.15, 0.67]	-.01 [-0.32, 0.38]

Note. ^{1}SWB refers to sum scores of 2 items. ^{2}SWB refers to sum scores of all four items. Significant effects highlighted in bold.

2.8 Discussion of Personality in Squirrel Monkeys

We examined personality structure in common and Bolivian squirrel monkeys. Personality traits in both species defined components labelled Agreeableness, Assertiveness, Neuroticism and Openness. Between-zoo comparisons revealed location differences in Neuroticism for common squirrel monkeys, and in Neuroticism and Agreeableness for Bolivian squirrel monkeys.

Male common squirrel monkeys scored higher than females on Assertiveness. Male Assertiveness scores increased with age, whilst the opposite was true for females. These findings support reports that males are dominant over females, in both captivity and the wild (Boinski et al., 2002). In Bolivian squirrel monkeys Openness decreased with age. As similar patterns have been found across multiple species (Donnellan & Lucas, 2008; King et al., 2008; Manson & Perry, 2013; Terracciano et al., 2005) this suggests that age-related declines in Openness are not specific to particular social systems. Female Bolivian squirrel monkeys were more agreeable than males, as has been found in humans (Soto, et al., 2011), chimpanzees (Weiss & King, 2015), and white-faced capuchins (Manson & Perry, 2013); there were no sex differences found in orangutan Agreeableness (Weiss & King, 2015). Sex differences in Agreeableness may therefore be an adaptation for living in large social groups. In Bolivian squirrel monkeys, the fact that females are philopatric and form female coalitions (Boinski & Cropp, 1999; Boinski et al., 2005; Boinski et al., 2002), may have provided selection for higher Agreeableness compared with males.

Of the two squirrel monkey species, Bolivian squirrel monkey components are more similar to those of brown capuchin monkeys. These results suggest that habitat differences may not influence personality structure. Instead, these similarities can probably be attributed to similarities in the social structures of brown capuchin monkeys and Bolivian squirrel monkeys, including the fact that both species have matrilineal societies (Boinski & Cropp, 1999; Boinski et al., 2005; Boinski et al., 2002), compete less for food resources than common squirrel monkeys do (Boinski et al., 2002), and exhibit male-only dispersal (Boinski et al., 2005). Previous findings in macaques have indicated that social structure may explain species differences in aggressive and dominant traits (Adams et al., 2015). Another possibility is that, as Bolivian squirrel monkeys were the first clade to diverge from the *Saimiri* genus (Chiou et al., 2011), they share more ancestral traits with species in related genera than do common squirrel monkeys.

At the level of single components, common and Bolivian squirrel monkeys had Neuroticism and Agreeableness components that were more similar to one another than either was to components in brown capuchin monkeys. On the other hand, for both squirrel monkey species, Openness and Assertiveness were more similar to their brown capuchin monkey counterparts than they were to their counterparts in the other squirrel monkey species. These results suggest that Assertiveness and Openness may be ancestral to all three species, whereas Agreeableness and Neuroticism are derived in *Saimiri*. Comparisons with other closely related species, such as the *Aotus* genus, as well as with more distantly related Neoptropical monkeys, such as *Alouatta, Saguinus* and *Callicebus* genera

(Opazo et al., 2006; Schneider & Sampaio, 2015), would be useful to corroborate this finding.

We predicted more similarity in aggressive traits between Bolivian squirrel monkeys and capuchins than between Bolivian and common squirrel monkeys, or capuchins and common squirrel monkeys. Whilst both squirrel monkey species appear to share assertive traits with capuchins, capuchin Assertiveness correlates more highly with Assertiveness in Bolivian squirrel monkeys than common squirrel monkeys. It is also notable that traits such as *aggressive* and *bullying* load on Assertiveness for both Bolivians and capuchins, whilst for common squirrel monkeys they load on Openness. This lends some support to our prediction that Bolivians are more similar to capuchins for traits relating to aggression and competition.

Five components---Neuroticism, Openness, Assertiveness, Agreeableness and Decisiveness---described personality structure at the genus-level. Decisiveness was comprised of items related to Assertiveness and Neuroticism items in Bolivian squirrel monkeys, and items related to Assertiveness and Openness in common squirrel monkeys. Of the two squirrel monkey species, the personality structure of common squirrel monkeys more closely resembled the genus-level structure. This suggests that as Bolivian squirrel monkeys diverged earlier from the *Saimiri* genus (Chiou et al., 2011), they have fewer traits in common with the other *Saimiri* clades than common squirrel monkeys do. Furthermore, congruence in item loadings between common squirrel monkeys and Bolivian squirrel monkeys was even lower than between each species and the genus-level structure. These results indicate that the personalities of Bolivian and common squirrel monkeys have diverged since they shared a common ancestor, although it appears that Bolivian squirrel monkeys retain more ancestral traits. As there are four main clades with varying social structures in the *Saimiri* genus (Boinski et al., 2002; Chiou et al., 2011), it would be useful to compare trait differences between them all to examine to what extent each species has retained ancestral traits.

For the genus-level components, common squirrel monkeys were lower in Agreeableness than Bolivian squirrel monkeys, which could reflect higher levels of in-group competition in common squirrel monkeys (Boinski et al., 2002). However, contrary to our prediction, the two species did not differ in Assertiveness. We found no sex difference in Assertiveness for either species, even though observations in the wild and captivity report sex differences in dominance for both common and Bolivian squirrel monkeys (Boinski et al., 2002). This result contrasts with findings in other species such as chimpanzees (King et al., 2008) and orangutans (Weiss & King, 2015), where males are higher in dominance. We did find species-specific sex differences for two components: common squirrel monkey males were higher in Neuroticism and Decisiveness than females, whereas in Bolivian squirrel monkeys, females were higher on these components. Male chimpanzees, and male white-faced capuchins, are higher in Neuroticism than females (King et al., 2008; Manson & Perry, 2013), although this trend is the opposite in humans (Soto et al., 2011). These findings may reflect the rank-related roles of males and females within different social structures. High dominance rank can be associated with higher stress levels, especially during periods of group change when social hierarchies are unstable

(Sapolsky, 2005). Thus it is possible that in squirrel monkeys, the more dominant sex exhibits more tendencies related to stress, negative affect, and anxiety; to determine whether this is the case would require examination of rank-related differences in Neuroticism and similar traits.

2.9 Discussion of Well-being in Relation to Personality

For common squirrel monkeys, we excluded two items, *goals* and *be monkey*, from further analysis due to low inter-rater reliability. The fact that only two of the well-being items were reliable is inconsistent with previous research, which has shown all four items to be reliable and to load on one component (Weiss et al., 2009; Robinson et al., 2016). This is likely a result of our small sample size, given that these items were reliable for Bolivian squirrel monkeys for which we had more than double the sample size. Consistent with our predictions, well-being in Bolivian squirrel monkeys was negatively correlated with Neuroticism and positively correlated with Openness. Although not significant, we also found a positive correlation between Assertiveness and well-being in common squirrel monkeys. Similar associations have been found between Neuroticism and well-being in humans (DeNeve & Cooper, 1998; Steel et al., 2008), chimpanzees (Weiss et al., 2009), orang-utans (Weiss et al., 2006), and macaques (Weiss, Adams, et al., 2011). Well-being has also been positively associated with Dominance and Openness in chimpanzees (King & Landau, 2003; Weiss et al., 2009) and with Assertiveness in brown capuchins (Robinson et al., (2016); see Appendix D)[8]. These data also help to put well-being assessment into a broader context. The structure of well-being appears to be similar across primate taxa, and shows similar associations to personality in both Old World and New World simians. This suggests that associations between personality traits and well-being may be ancestral to the split of the Platyrrhines and Catarrhines, around 43.5 mya (Perelman et al., 2011).

2.9.1 The role of well-being measures in welfare management.

Personality traits are correlated with response to both the social and physical environment, for example, how individuals respond to enclosure enrichment (Gartner & Powell, 2012) or interact with group members (Schel et al., 2013). In turn, well-being ratings have been found to correlate with ratings of welfare in brown capuchins (*Sapajus apella*), a measure that assessed social interactions, physical health and ability to cope with stress (Robinson et al., 2016). Thus, both well-being and personality assessment should be of interest to welfare management. The well-being questionnaire could be a quick and useful way to assess how individuals are coping in captive environments, and could be used to monitor changes over time and in response to new enclosures or changes in group composition.

An additional, important consideration for many zoos is the use of captive breeding programmes for conservation, which rely on good survival rates to succeed. As stress is known to increase mortality rates in captivity (Carlstead,

---

[8] I was involved in the conceptual planning and discussion of this study and provided the idea to include well-being assessment alongside welfare assessment, as well as assisting with statistical issues and manuscript edits.

Fraser, Bennet, & Leiman, 1999), addressing the role of personality and well-being on stress and longevity (Weiss, Adams, et al., 2011; Weiss et al., 2013) could benefit individual welfare and help to maintain healthy, breeding populations.

2.10 Future directions

This study is not without its limitations. Our sample size was smaller than we would have hoped. Because keeper time is limited, many zoos struggled to provide ratings, as it takes time to learn to distinguish between individual squirrel monkeys, and to provide ratings on them. Thus many zoos were unable to participate, or could only provide ratings on a few easily identifiable individuals. Although we were careful to provide bootstrapped confidence intervals for our regression analyses examining age and sex effects on personality, we should be cautious of our interpretation of the interaction effects given their low power.

An additional point of consideration is the extent to which we interpret these data to be representative of squirrel monkey species as a whole. Whilst we make the assumption that the differences between our captive samples of common and Bolivian squirrel monkeys reflect differences found at the species level, we should be cautious about the interpretation of such data without expansion of our sample. For example, to ensure that our findings accurately represent species-level differences, examination of these traits would be beneficial not only in more captive individuals but also in wild populations, particularly drawing direct behavioural comparisons of key traits, such as dominance or activity, between species groups.

Despite these limitations, the assessment of personality in captive primates continues to expand, and this study contributes data from two species of New World monkey not previously assessed using the HPQ. Whilst this study helps to further our knowledge about trait phylogeny, we recommend further exploration of what might determine species differences in personality in squirrel monkeys, such as through examining rank data and aggression frequency in relation to component scores. Expanding personality assessment to other species of New World monkeys would also help to establish whether these traits have diverged from a common ancestor with Catarrhines, or whether similar traits have occurred amongst Platyrrhines and Catarrhines through convergent evolution.

We particularly encourage further research in New World monkeys. As the assessment of personality in primates expands, it is becoming clear that these data further our understanding of how selection played a role in personality development. As demonstrated here, these data can help determine the extent to which traits are ancestral, and identify selection pressures that may have resulted in species differences. Expanding this approach further will no doubt help to increase understanding of the phylogeny and evolution of personality across primates and other animals.

Chapter 3. Using personality to model behavioural extremes

> *"One cannot escape the conclusion that every chimpanzee must possess a distinct personality."*
>
> - Meredith P. Crawford (1937, p. 79)

3.1 Chimpanzees as a Focus Species

The study of chimpanzee personality dates back to the 1930s, when researchers including Meredith Crawford and Robert Yerkes acknowledged the differential behaviour of chimpanzees (Crawford, 1938; Yerkes, 1939). Despite this early interest, the number of studies on primate personality published in the 2000s comprises approximately the same number of studies published between the 1930s and 1990s (Freeman & Gosling, 2010). The expansion of this field followed the seminal research by Stevenson-Hinde and colleagues, which assessed personality traits in rhesus macaques (Stevenson-Hinde & Zunz, 1978). Rhesus macaques remain the most studied primate species in personality research, likely because they are the most commonly kept captive primate. The second most studied species is the chimpanzee, making up 21% of all primate personality studies by 2010 (Freeman & Gosling, 2010). Chimpanzees, alongside bonobos, are our closest extant relatives, diverging from humans less than 6.3 million years ago (Patterson, Richter, Gnerre, Lander & Reich, 2006). They have been the subjects of a large body of research examining in what ways they are similar to, and differ from, humans (Call & Tomasello, 2008; Goodall, 2000; Kawai & Matsuzawa, 2000; Matsuzawa, Tomonaga & Tanaka, 2006; Tomonaga et al., 2004; Whiten, McGuigan, Marshall-Pescini & Hopper, 1999). From this research we know that chimpanzees use tools, can learn to use symbols and tokens, and have highly developed socio-cognitive abilities, including the ability to understand intent in others, and using gaze and gestures to communicate with others (see Figure 3.1). Given the similarities between chimpanzee and human cognition, it makes sense that efforts to assess personality in nonhuman primates have often focused on chimpanzees.

Figure 3.1

Chimpanzees show many behavioural and cognitive parallels to humans. They form friendships which are reinforced through social grooming (left), can solve problems using touch screen (centre) and use tools to access food (right).

3.2 The Comparative Approach

The expansion of personality assessment using the top down approach – i.e., deriving items from humans and applying them to other species – allows comparison of component structures across species. Differences in structure allow us to determine species-specific components, as well as traits that appear to be ancestral to multiple taxa. This not only helps us to put human personality into context, in considering how and why certain traits occur, and which traits we share with other species, it also allows us to address potential species-specific selection pressures, such as differences in social structure, that could help us to understand the evolution and diversity of personality.

In 1997, King and Figueredo published an assessment of personality in 100 captive chimpanzees. They measured personality using a 43 item questionnaire, with all but three items derived from Goldberg's Big Five (Goldberg, 1990) (see Chapter 1, and Table 2.1). The aim of this paper was two-fold: to (1) examine whether chimpanzee personality could be rated reliably, and (2) to examine how closely personality structure in chimpanzees resembled the five factors found in humans. Results revealed a six-factor structure, bearing similarities to the five factor structure seen in humans. Chimpanzees, similar to humans, have factors of Extraversion, Conscientiousness, Agreeableness, Neuroticism and Openness. In addition, they have a sixth factor, Dominance. The component structures, and similarities to humans, are described in Table 3.1. This structure has since been replicated in two independent samples (King et al., 2005; Weiss et al., 2009). The former study collected data from 117 chimpanzees at nine zoos in the US and Australia, and from 43 chimpanzees at a sanctuary in the Republic of the Congo, using the original 43 item questionnaire (King et al., 2005).

Although this study also found six factors, a later attempt to replicate this structure in chimpanzees resulted in only four factors, suggesting that Neuroticism and Openness were under-represented by items in the questionnaire (Weiss et al., 2007). Thus a more expansive questionnaire, consisting of 54 items, was developed, labelled the Hominoid Personality Questionnaire (HPQ) (Weiss et al., 2009). This was validated in a sample of 146 chimpanzees at ten facilities in Japan, and was consistent with earlier studies in revealing the same six personality domains.

This structure has been further validated against behaviour observations (Pederson et al., 2005) and traits have been found to show similar age and sex effects to humans, as well as showing similar associations with subjective well-being (King et al., 2008; King & Landau, 2003; Weiss et al., 2009). These findings present strong evidence that chimpanzees share with humans a similar life history of personality traits, making them a good candidate for comparative assessment of other traits.

3.3 Using personality assessment to understand behavioural extremes

Maintaining species typical behaviours is a paramount consideration when keeping animals in captivity (Davenport & Menzel, 1963; Mason, Clubb, Latham & Vickery, 2007). As demonstrated by Harlow, the developmental environment can have important influences on behaviours (e.g., Harlow, 1958). Animals that lack basic needs such as a suitable physical and social environment or lack of stimulation can develop atypical or extreme manifestations of behaviour.

Table 3.1

Factor structure from King & Figueredo (1997) for items derived from human personality assessment for use in chimpanzee assessment

	Item loadings	
Personality factor	Negative	Positive
Dominance	Submissive	Dominant
	Dependent	Independent
	Fearful	Decisive
	Timid	Intelligent
	Cautious	Persistent
		Bullying
		Stingy
Surgency	Solitary	Active
	Lazy	Playful
	Depressed	Sociable
		Friendly
		Affectionate
		Imitative
Dependability	Impulsive	Predictable
	Defiant	
	Reckless	
	Erratic	
	Irritable	
	Aggressive	
	Jealous	
	Disorganised	
Agreeableness		Sympathetic
		Helpful
		Sensitive
		Protective
		Gentle
Emotionality	Excitable	Stable
		Unemotional
Openness		Inventive
		Inquisitive

Note. Factor labels used here differ from more recent versions, which is reflected in the text. Differing factor labels include: Surgency = Extraversion, Dependability = Conscientiousness, Emotional Stability = (inverse) Neuroticism.

In captivity, chimpanzees that were deprived of social contact early in life have been observed to exhibit impaired social behaviour, excessive caution to novel objects, and peculiar, atypical behaviours that are often repetitive (Davenport & Menzel, 1963; Kalcher, Franz, Crailsheim & Preuschoft, 2008; Reimers, Schwarzenberger & Preuschoft, 2007; van Ijzendoorn, Bard, Bakermans-Kranenburg & Ivan, 2009).

Similar behaviours have been observed in the wild in orphaned infant chimpanzees (Goodall, 2000). Whilst it is clear that in apes, atypical behaviours can occur as a result of the environment, there has been little assessment of what other variables may cause atypical behaviours. For example in humans, neurodevelopmental disorders, such as autism spectrum disorder (ASD), can lead to deficits in social behaviour and communication, atypical idiosyncracies and trait extremes, such as Savantism (DSM-IV-TR: APA, 2000). To understand potential parallels between these extremes in humans and chimpanzees, we used personality ratings of chimpanzees to try to identify within-trait variation that could indicate potential underlying deficits. The following publication uses personality ratings to develop a new measure for identifying 'autistic-like' traits in chimpanzees[9]. In Chapter 4, we then examine behavioural correlations of this measure, to determine to what extent it represents frequency of observed behaviours, which may reflect trait extremes.

The following content has been published in:

Springer Science+Business Media New York / *Organism Models of Autism Spectrum Disorders*, Neuromethods vol. 100, 2014, p283 - 302, Social Relationships in Nonhuman Primates: Potential Models of Pervasive Disorders, Vanessa A. D. Wilson and Alexander Weiss; with kind permission from Springer Science and Business Media.

---

[9] The book chapter was the idea of A. Weiss, and was written primarily by myself with his guidance.

Social Relationships in Nonhuman Primates: Potential Models of Pervasive Disorders

Introduction

This chapter describes a holistic approach for studying neuro-developmental disorders related to autism in nonhuman primates. To understand the role of social behaviour in neurodevelopment, it is necessary to start with a basic understanding of the traits that define human autism. This gives us a basis for building the case for autistic traits in other primates. To establish how these traits might manifest in other species, we will consider the role of social structure and social knowledge on species' behaviour. We will also discuss rearing environment as a means of understanding behavioural differences in traits related to autism. Using chimpanzees as a preliminary model, we will assess personality traits that possibly reflect an autism spectrum, and discuss the implications of these findings for a non-invasive approach to model pervasive developmental disorders.

Why study social behaviour?

Behavioural observations complement neurodevelopmental studies. Studying neurodevelopment may advance our knowledge of brain structure and development, but is hard to apply to ape species for which invasive research is restricted for ethical reasons. Primates have been proposed as an ideal study species for invasive studies of neurodevelopment (Watson & Platt, 2012). However, we suggest that researchers must first rely on behavioural observations for understanding developmental deficits. Pairing neurodevelopmental models within a behavioural context will help define the term ‘neurodevelopmental deficit’ and thus enable such deficits to be addressed from the outside, in.

In this discussion we focus on primate models of autism. If autistic traits were only studied neurologically, this would not improve our understanding of autistic behaviours. On the other hand, by simply labelling behaviours as autistic, we do not gain an understanding of the neurology underlying the condition. We hope to resolve this by addressing behavioural deficits in respect of neurodevelopmental models. Brain stimulation studies have shown links between neural loci and emotive circuits in other mammals, resulting in consistent behavioural patterns (LeDoux, 2000; Panksepp, 1982). This work provides reliable indicators of internal emotive circuits based on behavioural recordings, from which we can try to interpret what an animal feels in specific situations (Panksepp, 2011). Using a similar approach, autism can be understood in more depth by building on neurodevelopmental studies, to assess how it may manifest itself as traits in other species.

To examine autism in nonhuman animals, we must first establish what we mean by 'autism'. The diagnosis of autism in humans is currently based purely on behavioural criteria (Baron-Cohen & Belmonte, 2005). Autism is classified as a pervasive developmental disorder (PVD), as defined by the DSM-IV-TR (*The Diagnostic and Statistical Manual of Mental Disorders:* APA, 2000)[10]. A PVD is identified as ‘severe and pervasive impairment in several areas of development’ ((*The Diagnostic and Statistical Manual of Mental Disorders:* APA, 2000): 69). Under this heading, autism is

---

[10] At the time of writing, the DSM-IV-TR (2000) defined autism using the triad of impairments. Since then, this definition has been reduced to a dyad of impairments (DSM-5, 2013), however, the behaviours within these categories remain similar to those addressed in this chapter.

defined in the presence of a triad of impairments: social behaviour, communicative skills and stereotypic behaviour (see Table 1). In addition to these diagnostic criteria, symptoms may include a number of other behaviours, such as oversensitivity to sensory stimuli (*The Diagnostic and Statistical Manual of Mental Disorders:* APA, 2000), and cognitive development is often impaired. However some individuals, although they struggle with day to day tasks, are exceedingly skilled in a specific area, and have been described as savants (Grandin & Johnson, 2005).

Crucially, a large degree of variation is seen in symptoms of autism; in one extreme, individuals may be very able but lack good social skills; at the other extreme, symptoms may be severe to the point that an individual does not learn to speak, dress themselves or use the toilet. In addition, individuals who are not classified as autistic often display criteria on the threshold to diagnosis (Baron-Cohen et al., 2001) suggesting autism is the extreme manifestation of typical human behaviour. Thus the variety of diagnoses in between has designated autism as a spectrum disorder (*The Diagnostic and Statistical Manual of Mental Disorders:* APA, 2000). This must be kept in mind when assessing what traits might be defined as autistic.

With these definitions in mind, we aim to identify traits that would characterise autism in nonhuman species. This is problematic, given that autism is considered a human disorder. Autism is associated with deficits in social cognition, such as a failure to demonstrate empathy and Theory of Mind (Baron-Cohen, 2000; Baron-Cohen, Leslie, & Frith, 1985). Theory of Mind refers to being able to infer the thoughts, feelings, beliefs, desires and knowledge of another (Baron-Cohen, 2000), and has been identified as one of the defining abilities of being human. Other species, such as chimpanzees, ravens and dogs, demonstrate aspects of Theory of Mind, including tactical deception and knowledge/intent attribution (Bugnyar & Kotrschal, 2004; Crockford et al., 2012; Schmelz, Call, & Tomasello, 2011; Viranyi, Topal, Miklosi, & Csanyi, 2006). Yet there is presently no evidence that they can understand the concept of false belief, as humans can, thus current definitions favour 'true' Theory of Mind as distinctly human (Call & Tomasello, 2008).

Autism is also implicated in abnormal brain growth in the neocortex (Pardo & Eberhart, 2007), an area strongly associated with human-specific cognitive abilities (Gibson, 2002). But what about evidence of neurodevelopmental deficits in other species? Mirror neurons are believed to play a role in human perception of others' actions, and have been implicated in structural deficits that determine perception of facial emotion in autistic children (Dapretto et al., 2006), although others have questioned this (Southgate & Hamilton, 2008). Given that mirror neurons have been found in macaques (Ferrari, Gallese, Rizzolatti, & Fogassi, 2003), it is logical to suggest that deficits in these regions may inhibit perception and species-typical behaviour.

Recent work in mice has established behavioural assays for testing target genes for autism (Silverman, Yang, Lord, & Crawley, 2010). These assays identified specific social interactions, communicative behaviour and stereotypies, believed to be developmental parallels with those seen in humans. Parallel evolution predicts that we would expect to find many behavioural and cognitive similarities between humans and other species, especially primates; developments in personality and cognition would support this (King & Figueredo, 1997; Tomonaga et al., 2004). It thus follows that we may find behavioural parallels for pervasive developmental disorders such as autism.

Social deficits observed on the autistic spectrum are central to its diagnosis in humans. Given that a variety of complex social structures exist in nonhuman primates (Kappeler & van Schaik, 2002), our close nonhuman relatives may act as a model for understanding how or why these social deficits develop. To address these deficits, we must ask how autism would manifest itself in other species. That is to say, if we looked for autistic traits in chimpanzees, what would we look for?

The importance of social relationships, communication and group knowledge

To examine autistic traits in chimpanzees, we must consider the idea of social structure in detail. Something that humans share with many primate species is group living, and the social interactions that come with it. The structures and organisations of primate social systems are complex and vary widely (Smuts, Cheney, Seyfarth, Wrangham, & Struhsaker, 1987): The fission-fusion groups of chimpanzees and capuchins*;* the semi-solitary lifestyle of orang-utans; the gorilla harem and pair-bonded douroucoulis; gelada and baboon troops made up of multiple sub-units. These are just a few examples of broad variation in social structure. All social groups form a web of interlinked components, including group size, male-to-female ratio, mate choice, mating system, sexual dimorphism, male-female dispersal, and social hierarchy.

Ecological and behavioural constraints determine individual interactions that form a group, but the group, in turn, constrains individual behaviour (Kappeler & van Schaik, 2002). For example the costs of social living increase with group size as larger groups experience higher levels of competition and aggression (van Schaik, 1983). Social structure also determines behavioural differences between the sexes. South

American squirrel monkeys (*Saimiri spp.*) for example, are distinct in their social structure: *S. boliviensis* live in larger, female dominated groups, where females form coalitions and show more aggression to each other than in *S. sciureus* (Boinski et al., 2002). However in *S. sciureus*, males, instead of females, form coalitions, and show more aggression to each other than in *S. boliviensis* (Mitchell, Boinski, & van Schaik, 1991).

Social interactions are thus dependent on social structure. Recent research addressed the benefits to individuals of cooperative behaviour. Sussman and Garber (Sussman & Garber, 2011) showed that across 51 species, affiliative behaviour contributed up to 91.7% of social interactions. By comparison, antagonistic behaviour contributed to less than 1%. Where spatial foraging allows for lower feeding competition, the benefits of social interaction are higher to the individual, and become a focal consideration of group structure (Sussman & Garber, 2011). Understanding what drives group social structure and cohesion is key to establishing species and population differences in social behaviour (Kappeler & van Schaik, 2002). Only by defining species-typical behaviour can we then address individual and species differences in atypical behaviour.

One requirement of group living is information sharing. This is beneficial for communication about predators and food location, but can also lead to kleptoparasitic behaviour, a form of information ‘eavesdropping’. Spider monkeys, for example, use calls when foraging to manipulate group size. Individuals were more likely to emit food calls when there was an abundant resource, and groups of subordinate males called less frequently than groups of dominant males (Chapman & Lefebvre, 1990). This suggests that individuals used their knowledge not only of food availability but also of social rank to determine how to respond to resource availability. Since subordinate ranks experience higher interference competition (Chapman & Lefebvre, 1990; Murray, Eberly, & Pusey, 2006) if food is scarce, subordinates will try to minimise group competition by keeping this information to themselves.

Social rank is integral to group communication, and has formed the basis for studies of primate social knowledge. If getting along in a group means knowing your neighbours, then knowledge of "who's who" is beneficial to individual success in a group. This is especially true in a hierarchy, where dominance rank determines resource gain (Chapman & Lefebvre, 1990; Murray et al., 2006). Dominance rank in a female baboon hierarchy is determined by data on number of supplants, aggressive, and submissive behaviour (Silk, Seyfarth, & Cheney, 1999). Hierarchical structure therefore predicts not only resource use but also social behaviour. For example, higher ranking female baboons groomed significantly more with maternal kin than lower ranking females (Silk et al., 1999). Social knowledge is a useful tool by which individuals mediate their 'privilege' of resource use through monitoring others.

So what does 'knowledge' refer to? Knowledge of a conspecific's whereabouts should rely on relevant sensory information. In many primate species, vocalisations play a role in social interactions. Researchers can take advantage of this to test individual knowledge. Playback experiments in vervets and baboons that live in large troops consisting of smaller family units have shown that females understand and respond to vocalisations of conspecifics as social cues. Seyfarth and Cheney, who studied these social interactions for over twenty years, describe the role of social knowledge to an individual: “to achieve a complete understanding of her society… she must be able to step outside her own sphere of interactions and recognize the relations that exist among others…” ((Seyfarth & Cheney, 2005): 209). This ‘sphere’ refers to the female’s immediate matrilineal family, thus suggesting that females must become familiar with all other individuals in their troop. For the female, this involves observing the interactions of other individuals and inferring the appropriate associations. Thus, when she hears an anomalous call sequence, such as a subordinate individual threatening a dominant individual, this call sequence does not fit with the information that female retains on group social rank. Subjects will respond to an anomalous call sequence by looking toward the source for a longer time than when an expected call sequence is played (Cheney, Seyfarth, & Silk, 1995).

Other experiments suggest that baboons are able to interpret the direction of threat-grunts from a dominant female as context specific (a threatened versus friendly interaction). They adjust their behaviour as to whether they interpret these threats to be directed toward them (Engh, Hoffmeier, Cheney, & Seyfarth, 2006). These experiments demonstrate the role of social knowledge for group living. They also suggest the role of social inference in these interactions. As in other species however, there is little evidence that baboons can differentiate between what they know and what others know. This suggests they do not develop a Theory of Mind as humans do. It does, however, suggest that they have a rudimentary ability of perspective taking, that is, a basic level of intersubjectivity.

These findings suggest that social knowledge is an evolutionary precursor to Theory of Mind. This fits with the development of social interaction in early human development. Emotional intersubjectivity (Gomez, 1998) is present in infants from three months old, who attune to others' emotions using eye contact. Emotional intersubjectivity is the most basic human social interaction and is likely a precursor to cognitive intersubjectivity, or Theory of Mind. Cognitive perception begins its study in children from nine months old (Trevarthen, 1979). At this stage, children develop triadic interactions with other people, and rely on shared visual attention for communicating with others (Emery, 2000). By the age of four, children understand desires, and are able to attribute false-belief (Wimmer & Perner, 1983). It is during this stage of development that autism in humans may become apparent, with ToM deficits apparent in the diagnosis of autism in children (Baron-Cohen et al., 1985).

Evidence in apes also suggests they demonstrate advanced perspective taking. Gomez (Gomez, 1998) offered evidence of emotional intersubjectivity in infant gorillas, such as the use of persistent eye contact and elaborate repertoires to gain the attention of a human playmate. Chimpanzees parallel early human development in gaze following and in distinguishing between directed and non-directed gaze (Tomonaga et al., 2004). Chimpanzees can also attribute differences in knowledge between individuals (Crockford et al., 2012). However findings suggest chimpanzees do not develop shared attention (Tomonaga et al., 2004) or attribute false belief (Call & Tomasello, 2008), as humans do. This suggests that, although other primates differ from humans in their ability to perceive the thoughts and actions of others, they also share some of these abilities. Theory of Mind should thus not be defined as a purely human attribute, but as part of a spectrum of social knowledge, understanding and perspective taking. Using this definition, we can establish the importance of studying these abilities in other primates for understanding neurodevelopment. In using primate social relationships as a model for understanding neurodevelopment, we are trying to establish how autism would manifest itself in other species. We will consider examples of typical and atypical social behaviour in primates, and how these traits would fit within the current definition of autism. This definition is categorised into the triad of impairments, and in addition we will examine traits relating to three other aspects of behaviour: intersubjective and empathic behaviour, sensory sensitivity, and propensity for specific skill or focus in one area.

Autism: manifests of social deficits

We now return to our earlier question: If we looked for autistic traits in other primates, what would we look for? For ideas of how to approach such traits, we can draw on the observations of those who have studied great apes in the wild. Chimpanzees are an ideal study species: they are one of our closest relatives, have been studied extensively in both captivity and the wild (Bard et al., 2011; Mitani, McGrew, & Wrangham, 2006; Whiten, 2011) and much is known about their social behaviour and emotional expression (Goodall, 2000; Parr et al., 2007). Goodall (2000) describes chimpanzees' broad repertoire of social behaviours, which help to maintain group cohesion, and to reassure and reconcile. These include physical contact, such as patting, kissing and embracing; allogrooming; sharing food; showing concern towards others; and helping and protecting kin or companions during fights (Goodall, 2000). They also exhibit context-dependent vocalisations, with call production determined by social context such as the sex and rank of the individual (Slocombe & Zuberbühler, 2010).

We can group these behaviours into categories that fit within the definition of autism. We have already identified social behaviour (social interaction with peers; use of facial expression; sharing) and communicative behaviours (vocalisations; physical contact). Examples of stereotypic behaviour are described in situations where individuals experience severe stress. In the wild these examples are specific to infants who have lost their mother, and display behaviours such as rocking, staring, hanging upside down for long periods of time, as well as inappropriate social behaviour toward peers and adults (Goodall, 2000). In captivity, long-term effects of social deprivation are exhibited in fewer social interactions and subordinate behaviour of deprived individuals (Reimers, Schwarzenberger, & Preuschoft, 2007).

Based on these traits we can hypothesise what behaviours might highlight developmental deficits among chimpanzees. But species differences in social structure, as we have seen, are likely to influence how a trait of 'autism' manifests itself. Let us consider these traits in a less social ape. Orang-utans are mostly considered solitary except when mating and raising young, or when abundant resources may favour low levels of fission-fusion (van Schaik, 1999). Observations of social groupings led Galdikas (Galdikas, 1985) to describe them as semi-solitary apes. Solitary play is also observed much more in infant orang-utans (50% of observation time) compared to infant chimpanzees (15% of observation time) between aged ten and eleven months (Miller & Nadler, 1981). Allogrooming (grooming with another) is observed in orang-utans, but rarely outside the natal unit (Galdikas, 1995). In captive groups, adult and juvenile orang-utans are observed to spend approximately 50% of their time in social interactions. For juveniles this includes 24% of total time in contact play, and for adults, 10% of total time allogrooming (Edwards & Snowdon, 1980). Social behaviours amongst adults include hand fondling, touch, arm extension, grabbing and mouthing. Although social interactions are clearly a part of orang-utan behaviour, expected deficits in social behaviour may be less profound in these more solitary species.

However communication is a still a key behaviour for individuals to interact with mates, young and rivals. Orang-utans have a broad repertoire of communication, including facial expressions, touch and visual signals for such interactions (Liebal, Pika, & Tomasello, 2006). Thus deficits of some aspects of social behaviour would still be expected in orang-utan neurodevelopmental disorders. The record of stereotypic behaviour in orang-utans is little documented in the literature, reflecting, perhaps, a difference in behavioural focus between species, rather than species-differences in behaviour.

Gorillas represent another social species with an alternative social structure. Gorillas live in harems, with females often transferring between groups, resulting in weak social ranks (Stokes, Parnell, & Olejniczak, 2003; Watts, 1994). This may result in the loss of maternal kin bonds, and could explain why few social interactions are observed between unit females (Parnell, 2002). Allogrooming in western lowland gorillas (*Gorilla gorilla gorilla*) is observed notably less than in mountain gorillas (*G. beringei beringei*), and is mainly only between mothers and infants. This is not because of an observed difference in social structure. Rather it is considered an effect of resting time and adherence of plant species to hair in the mountain gorillas (Parnell, 2002), leading to an increased frequency of allogrooming. These species differences in social behaviour are important considerations for predicting behavioural deficits.

Although social interactions do not seem as important to gorilla group life as they do for chimpanzees, as with orang-utans, communication is still a necessary part of these interactions. Gorillas are observed to use a variety of context-dependent close calls, and frequency of usage varies with dominance rank of both those giving and receiving the call (Harcourt & Stewart, 1996). Gestural communication has also been observed in captive gorillas (Genty, Breuer, Hobaiter, & Byrne, 2009), and is thought to be used to signal intent. Atypical behaviour has been documented in captive gorillas; infants that are hand reared by people show more solitary play and aggression than those reared by their mothers, however interacting with group members helped to mitigate these effects (Meder, 1989). Stereotypic behaviours observed in these infants include rhythmic body movements (such as rocking) and finger sucking; the frequencies of these behaviours increased when an individual was under stress, such as when introduced to conspecifics.

We have now established species typical behaviours and how they differ as a function of social structure. From this, we have deduced atypical behaviour under the triad of impairments. What about other aspects of autism? Deficits in empathic behaviour are harder to address; empirical studies of empathy in primates are few (Anderson, Myowa-Yamakoshi, & Matsuzawa, 2004; O'Connell, 1995; Parr, 2001). However observations of concern towards others (Goodall, 2000) and perspective taking in chimpanzees (Call & Tomasello, 2008), would predict lower perceptual abilities with neurodevelopmental deficits.

Savantism, the propensity for a focused skill or hobby, is also difficult to address. We must consider skill use within species' societies, such as tool use to obtain food or completing a problem-solving task in the lab. As with humans, some apes are smarter than others, referred to as 'geniuses' of the ape world (Herrmann & Call, 2012). In examining 'savant' like behaviours in apes, we may consider not just intelligence, but look for focused, skilled and repetitive behaviour typical to savantism.

A final consideration is sensory sensitivity. Autistic children can be sensitive to a variety of sensory stimuli (Watling, Deitz, & White, 2001). In working with autistic children, the author has observed every day sensations, such as touch, loud noises and even wearing clothes, can be distressing for individuals. They can become highly stimulated by detailed movement, such as the movement of a lift or a bag blowing in the breeze. Response to sensory stimuli may be classified as stereotypic, with stimulation involving repetitive behaviours such as hand flapping, rocking, and jumping up and down. In primates, repetitive behaviour is seen in response to a lack of environmental stimuli (for a review see (Ridley & Baker, 1982)). We may consider sensory sensitivity in primates a type of stereotypic behaviour, predicting an increase in fearful behaviours as well as a withdrawn interest in the environment, as behavioural deficits.

From the evidence reviewed here, stereotypic behaviours appear to occur under situations of social stress or lack of appropriate social interaction (Meder, 1989; Reimers et al., 2007). They have also been mainly documented in ape infants. If we are to establish behavioural parallels between the triad of impairments found in autistic humans, and behavioural deficits in nonhuman primates, care must be taken in how to interpret this behaviour. This can be understood in more detail by examining the work of Harlow and his colleagues.

Harlow demonstrated in infant macaques that social deprivation from birth has severe behavioural consequences (Harlow, 1958; Suomi & Harlow, 1972). Monkeys raised alone exhibited inappropriate aggressive behaviour when housed with conspecifics (Mitchell, Raymond, Ruppenthal, & Harlow, 1966), and females raised without mothers specifically showed a lack of maternal behaviour. This included disinterest towards the infant, lack of maternal contact, and indifference to having infants removed from their cage, as well as aggressive behaviour to the point of infanticide (Ruppenthal, Arling, Harlow, Sackett, & Suomi, 1976). These studies were the first to address the role that social attachment plays in individual social behaviour, and demonstrate more drastically the atypical behaviours observed in wild and captive apes.

Research into deprivation extends beyond behaviour observation. A study examining social deprivation in rhesus macaques found structural differences in the brains of socially deprived individuals compared to socialised monkeys (Martin, Spicer, Lewis, Gluck & Cork, 1991). Differences were found in the basal ganglia; in the caudate nucleus, which is implemented in learning, especially feedback processes; in the putamen, which regulates movement; and in the nucleus accumbens, which is involved in reward, addiction, aggression and fear. These findings suggested that abnormal sensory input in developing infants permanently affected the neurochemical structure of brain regions affected by social and environmental stimuli.

Interpreting atypical behaviours thus advocates caution (Ridley & Baker, 1982). Although stereotypic behaviours have been well observed, little is understood of the mechanisms that cause them (Gross, Engel, Richter, Garner, & Wurbel, 2011). A trait that may appear as a neurodevelopmental deficit, such as lack of social interaction or stereotypic behaviour, may in fact be the result of environmental deprivation, such as infant isolation or traumatic captive experience. In people it is clear that stereotypic and atypical social behaviour can develop from neglect, abuse or trauma during childhood (Perry, Pollard, Blakley, Baker, & Vigilante, 1995), or as a result of atypical neurodevelopment, as seen in children with autism (*The Diagnostic and Statistical Manual of Mental Disorders:* APA, 2000). In primates, these atypical behaviours clearly develop during socially deprived circumstances. However it is possible that stereotypies also occur naturally, as a result of neurodevelopmental deficits. We outline the predicted associations between atypical behaviour and neurodevelopment in Figure 1.

Given the potential similarities of behavioural deficits derived from different origins, it is crucial to take individual history into account when examining the manifestation of any such 'autistic' trait. Table 1 considers these behaviours in more detail, and documents examples of behavioural deficits in both wild and captive apes. Based upon these behaviours, we can hypothesise what behavioural deficits we might expect to find as a result of neurodevelopmental deficits (see Table 2). Predicted traits are taken from items on the Hominoid Personality Questionnaire (HPQ (Weiss et al., 2009)) and are grouped triadically as in the diagnosis of human autism.

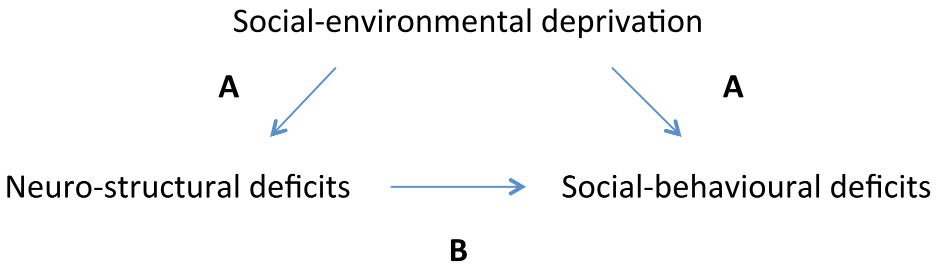


Figure 1

Origins of stereotypy in primates. Diagram A demonstrates the established associations between sensory input (social deprivation), behavioural response and neurodevelopment. Diagram B demonstrates the predicted effects of neurodevelopmental deficits on behaviour.

Table 1

Behavioural deficits and response to trauma as detailed in three species of apes

Neurodevelopmental deficits typical of autism in humans	Triad grouping	Nonhuman Primates	Behavioural deficits resulting from trauma, social isolation and poor living conditions	
			Behavioural deficits in captivity	Behavioural deficits in wild
Impaired social behaviours, such as lack of eye contact or recognition of facial expression; failure to interact socially with peers or to participate in joint activities; inability to recognise facial expression[5]	Social interactions[1]	Chimps	Timid; subordinate; few social interactions, incl. aggression, play, submission & affiliation, with higher stress[1]	Depression; over-aggressive towards/lack of play with, peers; (response of infants to loss of mother[2])
		Orang-utans	Increased contact with mother after mother infant separation[11]	No documentation found
		Gorillas	More solitary play, less social play, more aggression in hand-reared infants[9]	No documentation found

Lack of communicative skills, including delayed or complete lack of language development and repetitive use of language[5]	Communicative skills[1]	Chimpanzees	Lower levels of joint attention and cooperation, disorganised attachment at reunion[6]	Inappropriate submission to adults (response of infants to loss of mother[2])
		Orang-utans	Lower levels of socially mediated learning[8], infant-vocalised during mother-infant separation[11]	No documentation found
		Gorillas	Vocal distress upon mother-infant separation[13]	No documentation found
Repetitive behaviours, the need for very specific routines, distress towards sudden change[5]	Stereotypic/ atypical behaviours[2, 3]	Chimpanzees	Cautious response to novelty[1], non-social idiosyncracies[7,] rocking, freezing, object clutching[6], rhythmical and repetitive motions, posturing (taking peculiar stance)[10]	Rocking, hanging upside down motionless, pulling out & chewing hair[2]
		Orang-utans	Exhibit less activity in the absence of enrichment[3,4], increase	No documentation found

			in activity of infant following separation or death of mother[11,12], increase in non-active hanging after separation[11],	
		Gorillas	Exhibit less activity in the absence of enrichment[4], rhythmic body movement, finger sucking[9], increased activity in infants upon maternal separation, followed by self-holding, increased lethargy, decrease in play and curious behaviour[13]	No documentation found

Note. Behaviours documented include both initial response to trauma (e.g. separation) and established response to longitudinal conditions. Behaviours are divided based on the triad of impairments as classified in the human diagnosis of autism: social interactions, communicative skills and stereotypic behaviours. As observations for the remaining behavioural categories - lack of empathy/Theory of Mind[1], sensory sensitivity[2] and savantism[3] – are less documented in nonhuman primates, these behaviours are incorporated into the first three categories.
Data from (Reimers et al., 2007)[1], (Goodall, 2000)[2], (Tripp, 1985)[3], (Wilson, 1982)[4], (*The Diagnostic and Statistical Manual of Mental Disorders: DSM-IV-TR*, 2000)[5], (van Ijzendoorn et al., 2009)[6], (Kalcher et al., 2008)[7], (Descovich, Galdikas, Tribe, Lisle, & Phillips, 2011)[8], (Meder, 1989)[9], (Davenport & Menzel, 1963)[10], (Nadler & Codner, 1983)[11], (Whilde & Marples, 2011)[12], (Hoff, Nadler, Hoff, & Maple, 1994)[13], (Baron-Cohen, 2000)[14].

Table 2

Expected trait deficits in chimpanzees that would demonstrate neurodevelopmental deficits

Diagnostic Grouping	Expected trait deficits	
	Trait increase	Trait decrease
Social interactions*	Fearful Timid Solitary Aggressive	Dominant Stable Sociable Playful Affectionate
Communicative skills*	Submissive Quitting^{+}	Helpful Intelligent
Atypical behaviour*	Cautious Autistic Depressed Disorganised	Curious
Empathic Behaviour	Unperceptive	Sensitive
Sensory Sensitivity	Active^{+} Anxious	Active^{-}
Savantism	Individualistic Persistent	Quitting^{-}

Note. Predicted traits are taken from the HPQ (Weiss et al., 2009) and are based on behavioural deficits observed in both wild and captive situations. Similar traits are predicted to develop from either social-environmental trauma (as described in Table 1) or from neurodevelopmental deficits. Predicted trait changes are grouped according to human diagnostic criteria for autism.

*Indicates the triadic grouping of deficits. Thus items in each grouping refer to their usage in that context. Traits labelled +/- indicate those that may be exhibited in both extremes, as suggested by findings documented in Table 1.

Table 3

Sex differences in the Autism Scale for the whole sample; number of males and females in the upper and lower quartiles of the scale

	Upper quartile	Lower quartile
Males	19	11
Females	25	33

Individual differences: An empirical approach to defining nonhuman autism

In this preliminary assessment, we use chimpanzees as a model for assessing autism in primates. Personality research uses keeper-rated questionnaires to assess individual differences in primate personality. Ratings have found consistency across locations (King & Figueredo, 1997), have been behaviourally validated (Konečná et al., 2008), and have been correlated with scores of well-being (Weiss et al., 2009; Weiss et al., 2006). This study aims to examine personality traits as manifests of potential neurodevelopmental deficits. The HPQ is therefore an ideal tool for assessing atypical behaviour in chimpanzees.

Six raters were asked to rate items of the HPQ on a scale classifying their relation to traits of autism. Raters had between three and ten years experience with autism in humans. Experience included positions of care, education and academia. Items were assigned 1, -1, or 0. A score of 1 indicated a positive association of the item with autism, -1 indicated a negative association, and 0 indicated no association. For each item, mean ratings were taken. Personality ratings were available for 176 chimpanzees from 13 locations, with 58 raters providing ratings. Mean ratings of autism items were multiplied with individual chimpanzee item ratings, for all raters. The sum of all ratings per individual formed their autism scores per rater. The inter-rater reliability of autism scores defined by intraclass correlations (Shrout & Fleiss, 1979) was then assessed. The reliability of individual ratings or *ICC*(3,1) was 0.33. The reliability of mean ratings or *ICC*(3,k) was 0.61. A frequency plot determined that scores were normally distributed. An average score per individual provided us with individual ratings on an Autism Scale.

These ratings thus provide a possible reliable measure for assessing traits related to autism in captive chimpanzees. For a preliminary analysis of this scale, we controlled for sex and location of chimpanzee in a linear regression model. In humans, autism prevalence in males is around four times that in females (Yeargin-Allsopp et al., 2003). This sex difference is thought to derive from natural sex differences in behaviour (Baron-Cohen, 2002), as well as physiology, such as how the brain processes emotional expression (Schulte-Ruther, Markowitsch, Shah, Fink, & Piefke, 2008), suggesting that males are more predisposed to display autistic traits. Based on this we expect that males would be higher on the Autism Scale than females. The sex ratios in the upper and lower quartiles are presented in Table 3. We found a trend towards sex differences, with males being higher than females; however this was not significant, (b (1,162) = 0.24, t = 164, p = .10).

We examined mean trait differences for individuals in the upper and lower quartiles of the Autism Scale. Using these scores we assessed the predictions we made in Table 2 of expected trait deficits in individuals high on the scale. Table 4 outlines our findings relative to our predictions. Out of traits predicted to increase in those with a high autism rating, 10 out of 15 predictions were supported by our findings. These traits loaded across five out of six diagnostic groupings of human autism. For a predicted decrease in traits, only 3 out of 11 predicted traits were found to decrease. This included playful, which was classed under Social Interactions, curious, which was classed under Atypical Behaviour, and quitting, classed under Savantism. No predicted decrease was found for Communicative Skills, Empathic Behaviour, or Sensory Sensitivity.

Our predictions were built on previous findings of stereotypic behaviour, such as those induced by low environmental enrichment and social or emotional trauma. The low concurrence of our trait predictions with real trait loadings suggests that the traits exhibited are representative of an autism dimension, and not simply a result of trauma-induced stereotypy. This is notable in the items aggressive and cautious, which show high prevalence in wild and captive instances of atypical behaviour (see Table 1). These item scores were found to be lower in individuals in the upper quartile of the Autism Scale. Similarly, there was no decrease in dominance, stability, or activity, items associated with social deprivation and trauma. Item weights to create the scale are presented in Table 5. We previously expressed the need for caution in interpreting stereotypic behaviours in chimpanzees as autistic. While we still advocate caution, our findings tentatively suggest that it may be possible for individuals familiar with chimpanzees to rate them on something akin to the autism spectrum.

Based on these findings, we can compare trait deficits in the chimpanzee Autism Scale to those found in humans. Autism is strongly defined in people by atypical social behaviour. In chimpanzees, the findings suggest that sociable behaviours generally do not decline.

Although solitary loads in the top half of the scale, sociable and friendly also load in the top half, whilst playful loads in the bottom half of the scale (Table 5). Findings for Communicative deficits also differ from humans, in that traits did not differ in high-end individuals as predicted. This suggests that social and communicative interactions are not affected in the same way for chimpanzees as in humans.

However, high-end individuals do demonstrate atypical behaviour, with higher loadings on autistic and depressed than lower quartile individuals.

Table 4

Findings of predicted trait differences on the Autism Scale

Diagnostic Grouping	Predicted increase	Upper quartile increase	Predicted decrease	Upper quartile decrease
Social Interactions	Fearful Timid Solitary Aggressive	Fearful Timid Solitary	Dominant Stable Sociable Playful Affectionate	Playful
Communicative Skills	Submissive Quitting		Helpful Intelligent	
Atypical Behaviour	Cautious Autistic Depressed Disorganised	Autistic Depressed	Curious$^-$	Curious
Empathic Behaviour	Unperceptive	Unperceptive	Sensitive	
Sensory sensitivity	Active$^+$ Anxious	Active$^+$ Anxious	Active$^-$	
Savantism	Individualistic Persistent	Individualistic Persistent	Quitting	Quitting$^-$

Note. Changes in predicted traits were assessed as the difference between scorings on the upper and lower quartiles of the Autism Scale. Traits that were higher in the upper quartile were graded as Increased. Traits that were lower in the upper quartile were graded as Decreased.

Table 5

Trait loadings defined as the difference between trait means of upper and lower quartiles on the Autism Scale

Trait	Scores
Erratic	-0.291919192
Decisive	-0.227840909
Quitting	-0.214646465
Disorganised	-0.208459596
Bullying	-0.183901515
Jealous	-0.174494949
Predictable	-0.14040404
Unemotional	-0.083333333
Curious	-0.059027778
Playful	-0.053093434
Inquisitive	-0.04905303
Aggressive	0
Cautious	0
Conventional	0
Defiant	0
Dependent	0
Innovative	0
Submissive	0
Manipulative	0.007954545
Imitative	0.022916667
Inventive	0.024558081
Active	0.034848485
Dominant	0.063383838
Persistent	0.103282828
Independent	0.150883838
Intelligent	0.155618687
Cool	0.176262626
Stingy	0.191414141
Gentle	0.225757576
Helpful	0.236616162
Depressed	0.265972222
Thoughtless	0.265972222
Timid	0.270265152
Lazy	0.288510101
Distractible	0.293813131
Vulnerable	0.295770202
Protective	0.318939394
Sensitive	0.350757576
Friendly	0.386489899
Fearful	0.392424242

Autistic	0.394444444
Affectionate	0.423611111
Irritable	0.526388889
Sympathetic	0.539141414
Anxious	0.586994949
Stable	0.588257576
Clumsy	0.618371212
Reckless	0.85530303
Unperceptive	0.866666667
Sociable	0.936868687
Impulsive	0.94905303
Solitary	1.141414141
Excitable	1.479166667
Individualistic	1.511212121

Note. Scores that equal 0 are items that raters weighted 0.

Empathic behaviours also show a decrease at the high end, with high loadings of unperceptive and thoughtless. Sensory sensitivity found high loadings for active and anxious as predicted. And Savantism found high loadings for individualistic and persistent, as well as a decrease in quitting for high-end individuals. This suggests that in chimpanzees, traits manifest more strongly in the latter four groupings of behaviour than for Social and Communicative behaviours.

The next step for expanding on these results would be to examine what factors might cause these species-differences in trait manifestations. The influence of social structure and social interactions should be a key consideration in why chimpanzees and humans differ in the severity of certain trait deficits. Assessing these traits in other ape species with different social structure would also contribute to knowledge of autism differences between species. These differences make clear that it is crucial to understand species-specific information on social behaviour and cognitive skill before assessment.

In addition there are many factors not considered here which cannot be ruled out. This is especially important given that autism is a spectrum disorder defined by varying degrees of deficits. Assessment should address individual captive background, such as what environment an individual was born and raised in, and whether they have experienced any social trauma. One would expect these to have little impact on autism scores if these scores are a result of neurodevelopmental deficits. By using the Autism Scale presented here, we can address these traits in more detail and examine their influence on neurodevelopment.

Conclusion

Here we presented potential behavioural deficits in neurodevelopment for chimpanzees, and described the scores of these traits on a Chimpanzee Autism Scale. Far from arbitrary, these traits show similarities with deficits found in humans with autism, including higher autism scores in males. We suggest these traits are not simply deficits of environmental or social deprivation. This preliminary analysis advocates caution until further studies assess species and individual variation in these scores. Species social structure, cognition and individual background all must be taken into account when using this scale.

From these initial findings, we propose that the Chimpanzee Autism Scale may be a useful tool to assess atypical behaviours in chimpanzees. This will allow us to understand the neural basis of autism using non-invasive methods. Not only is this applicable to chimpanzee welfare, but it will help address the evolutionary proximity of chimpanzee neurodevelopment to that of humans.

3.4 Summary

In this chapter, we explored the use of personality ratings in chimpanzees to develop a scale by which to identify traits potentially indicative of atypical development. Our findings tentatively suggest that this scale could be applied to understanding behavioural deficits in chimpanzees. We argue in the above chapter that these ratings could be used to understand deficits that have resulted from atypical neural development, rather than environmental influences such as trauma or social isolation. However, it is important to consider that the two are often difficult to separate. For example, early social deprivation can cause long term structural differences in the brains of rhesus macaques (Martin et al., 1991). Maternal care can also alter gene expression and thus affect the regulation of endocrine and behavioural pathways (Meaney, 2001). Furthermore, the interaction of genes and environment means that the effect of an environment is sometimes dependent on which copies of a gene an individual carries (Suomi, 2006). In this case, it can be hard to treat neural development as an entity completely independent of environmental influence, without prior knowledge of genetic or environmental backgrounds. Thus, for this scale to be used to understand potential differences in neural development amongst individuals, would require careful consideration of each chimpanzee's background and rearing history.

Cautiously, these results suggest that there may be parallels in socio-behavioural deficits between humans and chimpanzees. These results reveal potential sex differences in behavioural deficits which reflect findings in humans: ASD is diagnosed more frequently amongst males than females (Yeargin-Allsopp et al., 2003). Although Lai et al. (2011) have suggested that this male-bias could be due to an under-diagnosis of autism in females, others have found that in a sample of non-autistic adults, males still score higher than females on traits associated with ASD (Baron-Cohen et al., 2001), supporting the theory that males are more predisposed to traits associated with autism (Baron-Cohen 2002). The similar pattern we found of sex differences for autistic-like traits in chimpanzees, suggests that underlying biological differences between the sexes may be to some extent ancestral, and are worth exploring in more depth. Ideally such research would examine how chimpanzee males and females differ in perspective taking and empathy tasks, parallel to work in humans (Baron-Cohen & Wheelwright, 2004; Frank, Baron-Cohen, & Ganzel, 2015; Schiffer, Pawliczek, Müller, Gizewski, & Walter, 2013).

It would be also be worth examining certain traits in more detail. We predicted differences in trait scores for chimpanzees at either end of the Autism Scale, based on atypical behaviour that results from early life trauma. We hypothesised that if our predictions about trait scores were not consistent with our findings, this could be indicative of atypical development resulting from non-environmental effects, rather than from environmental effects. Indeed, for many traits this was the case. For example, the trait cautious did not load highly on the Autism Scale. Chimpanzees who have experienced early social deprivation tend to exhibit more caution to novelty than their socialised counterparts (Reimers et al., 2007). The fact that cautious does not load highly suggests that a high score on this scale may be more likely to represent atypical development resulting from non-environmental effects. Similarly, other items, such as sociable and affectionate, did not load as one would expect as a result of early environmental trauma, with both these items showing high loadings on the Autism Scale. These findings suggest that the scale may be getting at something underlying behavioural deficits that is homologous to ASD in humans.

The problem with this interpretation is that the scale used in chimpanzees was designed with humans in mind. That is, each rater with experience of human autism, provided their item weights as to whether or not they believed each item to be associated with autism in humans. Thus, this limits the application of this scale to chimpanzees without providing validation of these scores. Examining behaviours associated with these traits – such as levels of agonism towards others, frequency of stereotypies and time spent with others – would provide a more detailed picture of whether these trait loadings accurately reflect underlying behavioural deficits. Assessing whether Autism Scale scores are good predictors of behavioural frequency would be a first step towards validating this scale. Additionally, it would be of benefit to examine whether other variables – such as age, sex, or personality measures – are stronger predictors of these behaviours than scores on the Autism Scale.

One question that we did not discuss in the above chapter is whether it would be possible to assess autistic-like traits in wild chimpanzees. Atypical behaviour has been observed in wild chimpanzees (Goodall, 2000; Ferdowsian et al., 2011), however, although we tend to assume such behaviours to be uncommon in the wild, the extent of their prevalence is essentially unknown (Brüene, Brüene-Cohrs, McGrew & Preuschoft, 2006). Observations indicate that, in relation to sanctuary-housed chimpanzees, the presence of atypical behaviours that parallel depressive/post-traumatic disorders in humans, are relatively low in wild chimpanzees (Ferdowsian et al., 2011). Yet a systematic assessment of such traits, and their origin, would be practically difficult in wild populations. For example, how can we assess the cause of an atypical behaviour without full knowledge of an individual's emotional and environmental experiences? We know that wild chimpanzees that suffer trauma, such as an infant losing their mother, can experience depressive-like behaviour (Goodall, 2000), but can such behaviour result in the absence of a trauma? Understanding the determinants of such traits in wild chimpanzees could help to place into perspective our knowledge of atypical behaviour in captivity. Yet, such an understanding, in contrast to captivity, is a challenging task, making such a question hard to answer.

We were fortunate to have access to both personality and behavioural data from a sample of 19 chimpanzees housed at Edinburgh Zoo. In the following chapter we explore whether scores on the Autism Scale are associated with behaviour, i.e. whether they might be indicative of behavioural 'extremes', or whether such behaviours are better accounted for by personality scores.

Chapter 4. Personality, Autistic-like traits, Stereotypy and Social Interactions in Captive Chimpanzees

> *"He had become a pathetic wreck of a chimpanzee, emaciated, lethargic, and morose…. Hunched up with his arms around his knees, he sat often rocking from side to side… he pulled out hair after hair, chewing at their roots, then dropping them."*
>
> \- Jane Goodall (2000, p.225)

4.1 Personality, Well-being and Welfare

Differential research has recently begun to explore the ways in which personality predicts responses to the environment – be it physical or social. In apes for example, higher Extraversion and Agreeableness predict higher well-being (chimpanzees: King & Landau, 2003; Weiss et al., 2009; orangutans: Weiss, King, & Perkins, 2006). In turn, well-being, and Extraversion, both have been associated with longevity (happier orangutans/more Extraverted gorillas, live longer) (Weiss et al., 2011; Weiss et al., 2013). Given that longevity is an important consideration for maintaining and breeding from captive populations, these findings should be of practical use for both welfare and breeding purposes within zoos. However, as yet we know little about the mechanisms that mediate the relationship between personality, longevity and well-being. Like personality (van Oers et al., 2005), well-being in humans appears to be heritable (Bartels, 2015; Lykken & Tellegen, 1996) and to share additive genetic variance with Neuroticism, Extraversion and Conscientiousness (Weiss, Bates, & Luciano, 2008). Similarly, well-being measures in chimpanzees share genetic variance with Dominance (Weiss, King, & Enns, 2002). If the same genes underlie both particular traits and happiness, then perhaps the functional mechanism that affects one also affects the others.

One possibility is that personality traits influence individual responses to social or environmental stressors. For example, social support received by extraverts could be protective against the effects of stress (Weiss et al., 2013). A recent study in goats lends support to this hypothesis: individuals with higher sociability measures showed significantly less variation in heart rate across behavioural contexts than individuals with low sociability scores (Briefer et al., 2015). Similarly in wild baboons, females who frequently spent time alone tended to have higher glucocorticoid levels, even when accounting for dominance rank (Seyfarth, Silk & Cheney, 2012).

Studies have also found that individuals differ in their response to the physical environment. For example in captive snow leopards, scores on ratings of Active/Vigilant and Curious/Playful were both associated with approaches and exploration of novel objects within their enclosure (Gartner & Powell, 2011). And in zoo-housed Diana monkeys, individuals that exhibited aggressive, irritable or solitary traits had increased levels of abnormal behaviour during high visitor density, whereas those monkeys that were active and playful showed an increase in species-typical behaviours, such as play (Barlow et al., 2006). Differences in response may indicate stress, as has been found in clouded leopards; fearfulness in this species has been associated with higher faecal corticoid concentrations, a marker of chronic stress (Wielebnowski et al., 2002). Such findings indicate the importance of accounting for individual differences when addressing how individuals respond to the environment.

Measuring how animals cope with a captive environment is the aim of animal welfare assessment (Broom, 1991; Hill & Broom, 2009), with attention paid to the animals' environmental, physiological and behavioural needs. In captivity, the social and physical environment of an animal may differ greatly from their species-typical environment. This can lead to stereotypical behaviour – repetitive, and often abnormal behaviours that may appear to have little function (Davenport & Menzel, 1963; Mason et al., 2007). Stereotypic behaviours range from repetitive motion (rocking, pacing) to self-directed behaviours (self-plucking, self-harming, regurgitation, faeces eating, urine drinking) to other-directed behaviours (over-grooming conspecifics, allo-plucking, excessive aggression) (e.g. Birkett & Newton-Fisher, 2011). Prevention and reduction of such behaviours are a priority for zoo welfare, which is why understanding risk factors that could lead to atypical behaviour is important.

Abnormal behaviour is influenced by both physical and social aspects of captive environments. For instance, agitated behaviour in captive black rhinos has been associated with number of enclosure walls (Carlstead et al., 1999) whilst single-housed female macaques show higher levels of stereotypy than females housed in social pairs (Eaton, Kelley, Axthelm, Lliff-Sizemore, & Shiigi, 1994). Social deprivation, particularly if experienced early in life, can cause long-term deficits in social behaviour and susceptibility to stress (Harlow, 1958). For example, during a re-socialisation period, chimpanzees who experienced early life social deprivation exhibited stereotypies included eating disorders (regurgitation, coprophagy), self-injury, dissociative and repetitive behaviours (Kalcher-Sommersguter, Franz-Schaider, Preuschoft, & Crailsheim, 2013). They also have higher glucocorticoid levels than their counterparts who experienced later life social deprivation (Reimers et al., 2007). It has also been observed that abnormal behaviour increases amongst chimpanzees transferred from a laboratory to a sanctuary environment, possibly as a mechanism of coping with the change (Kranendonk & Schippers, 2014). However, a longitudinal study suggests that rehabilitated chimpanzees do over time engage more in positive social behaviours with counterparts, a change which is more apparent in younger chimpanzees (Llorente, Riba, Ballesta, Feliu, & Rostán, 2015).

Whilst this research highlights the importance of environmental effects on behaviour, little is known about the degree to which susceptibility to stereotypic behaviours, which may occur in response to environmental triggers, depends on other variables, such as personality and coping mechanisms. Indeed, the diversity and frequency of abnormal behaviours exhibited by different individuals cannot be explained by their background, rearing history, age or sex (Birkett & Newton-Fisher, 2011), suggesting that other, differential factors are at work. The interaction between social and environmental influences, and behavioural and physiological outcomes, is an important consideration for maintaining happy and healthy captive populations. It is therefore of great relevance to welfare science to explore the ways in which personality predicts responses to the environment – be it physical or social.

Although previous work in primates has revealed associations between personality ratings and behavioural observations (Capitanio, 1999; Eckardt et al., 2015; Konečná et al., 2008; Morton, Lee, Buchanan-Smith, et al., 2013;

Pederson et al., 2005), the extent to which negative welfare indicators (such as stereotypies) and positive welfare indicators (such as social interactions, activity budgets) are influenced by personality is largely unknown. For example, are certain personality traits associated with higher levels of stereotypies, and if so, why might this be? Does this indicate a coping mechanism for higher stress levels that may be associated with certain traits? Personality assessment may also help us to clarify what 'positive' welfare means. For example, more introverted chimpanzees may naturally be less sociable, but this does not necessarily mean that they have negative welfare. Thus, understanding how personality relates to these behaviours could help to mediate the effectiveness of enrichment interventions which are used to increase positive welfare in captivity.

In the previous chapter I discussed the idea of using personality traits in chimpanzees as a tool for assessing behavioural deficits that are often seen in human neurodevelopmental disorders such as autism spectrum disorder (ASD) (Wilson & Weiss, 2015). The theory behind this was to take a comparative approach to understanding how and why disorders such as ASD occur, and whether they really are specific to humans, or whether similar behavioural deficits may also be seen in nonhuman primates. Given the similarities in social behaviour, such as affiliative behaviour, communication, maternal care and social cognition (Call & Tomasello, 2008; Matsuzawa, 2006; Pollick & de Waal, 2007; Romero, et al., 2010) that we share with chimpanzees, they may be an ideal species for understanding how deficits in social behaviour reflect personality or something akin to a neurodevelopmental disorder.

We proposed the use of personality items as indicators of 'autistic-like' traits in chimpanzees (Wilson & Weiss, 2015). This in no way means that we advocate that chimpanzees have autism or can be autistic, but simply that they may also exhibit deficits in social behaviour that are perhaps better explained in terms of internal rather than external factors. Here it is important to make a clarification: when we use the term 'internal' we refer to processes underlying behaviour, such as the genetic and neural basis of behaviour. By using the term 'external' we refer to processes existing outside of the body, such as social and physical environment, which can influence behaviour. It is evident that internal and external processes do not exist entirely independent of one another, for example, gene x environment interactions can produce differences in behavioural outcomes (Suomi, 2006; Capitanio et al., 2008). However, the typical assessment in welfare studies tends to address primarily external influences on behaviour without accounting for internal processes (Kalcher-Sommersguter et al., 2013; Kranendonk & Schippers, 2014). Here, we attempt to address this through the use of two measures that we take to represent internal processes, by examining whether these are perhaps a better explanation of certain behaviours than the immediate external environment.

In the following study we examined chimpanzees' scores on a composite of traits judged, in humans, to characterise autistic individuals, and chimpanzees' personality scores on the Hominoid Personality Questionnaire, in relation to behaviours exhibited within a captive group setting. We predicted that (1) if behaviours were exhibited as a result of neurodevelopmental deficits, we would expect to find the autism scores stronger predictors of specific behaviours than personality scores. (2) If behaviours were not exhibited as a result of neurodevelopmental deficits, but instead as a result of other internal processes, then we would expect personality to be a stronger predictor of these behaviours than autism scores. (3) If the immediate environment plays a stronger role in determining behaviour than internal variables, then we should find that neither personality scores nor autism scores are associated with these behaviours.

4.2 Methods

4.2.1 Subjects.

Subjects consisted of 19 adult chimpanzees including 11 females and 8 males, between 13 and 48 years old when data collection started (mean age = 26.53, *SD* = 10.20), housed at the Budongo Trail Exhibit, Edinburgh Zoo. The group was originally two separate groups, one from Edinburgh Zoo and one from Beekse Bergen Safari Park in the Netherlands. Prior to 2007, the latter group had been housed at the Biomedical Primate Research Centre in the Netherlands (Herrelko, 2011). The two groups were merged successfully during 2010 (Schel et al., 2012). The Budongo Trail facility consists of three connected indoor enclosures, each 12 x 12 x 14m, an outdoor enclosure covering 1832m^2, two conjoined research rooms totalling 26.5m^2, and off-show bedding area of 21.45m^2. Chimpanzees are free to access the indoor and outdoor areas as they choose, but access to the research rooms is restricted to research hours to increase the novelty of accessing this space.

4.2.2 Personality ratings and autism scores.

Personality ratings were collected for all 19 chimpanzees in 2010 (Herrelko et al., 2012). Data were collected using the HPQ, which is described in Chapters 2 and 3. Each chimpanzee was rated by between two and four raters (mean = 3.0, *SD* = 1.03). We assessed interrater reliability using the same method described in Chapter 2. We found three items to be unreliable (less than or equal to 0) – these included *impulsive, predictable* and *clumsy*. Components were scored using the structure in Weiss et al. (2009), the only difference being that we excluded the unreliable items (see Table 4.3). This produced six components, labelled Dominance, Extraversion, Conscientiousness, Agreeableness, Neuroticism and Openness. We calculated mean score per individual and scaled all six variables for analysis.

We used the weighted scores developed in Chapter 3 to calculate an individual 'autism score' for each chimpanzee from the personality ratings.

4.2.3 Behaviours.

For this study we utilised behavioural data collected for the long term data set on the Budongo chimpanzees. Behavioural observations were taken of the chimpanzees between July 2012 and March 2013 for a total of 67 observation days. Each observation period lasted between 10 and 30 minutes with up to eight observations per day. Observations took place at one location in the enclosure (e.g. pod 1) for no more than 30 minutes and observers could not return to the same location within 30 minutes after the end of the last observation period. Each observation period began with an instantaneous group scan, for which the behaviour of each individual present was recorded at that time point. Behaviours recorded included rest, self-groom, forage, eat, travel, climb, play, give grooming, receive grooming, mutual grooming, fight and other. This was followed immediately by a 10 minute focal observation period during which we noted proximity to nearest neighbour, eating, stereotypies, grooming and displacements (see Ethogram in Table 4.1). Focal individuals were chosen based on a record of who had not been recently observed, and based on who was available at each location. The end of each focal was followed by a group scan. Within this observation period, detailed records of grooming and aggression behaviours were also recorded (see Ethogram in Table 4.2 for grooming behaviours) on an all occurrence basis (Altmann, 1974) for all individuals present in that area. Data were jointly collected by eight researchers who were trained in the data collection process, and were required to pass a chimpanzee ID test prior to commencing data collection. Following training, in initial data collection, a new researcher would observe the chimpanzees alongside an experienced researcher, and both would simultaneously record the same behaviours. Data were compared between researchers to ensure consistency before the new researcher started to collect data alone.

For this study we chose to focus on social and stereoptypic behaviours – both important considerations in assessing atypical behaviour in captivity (Birkett & Newton-Fisher, 2011; Kalcher-Sommersguter et al., 2013). The behaviours we focused on included regurgitation and faeces eating, both available from the focal data. To examine social behaviour, we examined neighbour proximity (focal data), instances of social vs. self grooming (scan data), direction of grooming (scan data) and duration of grooming (grooming data). We chose these measures as proximity and grooming are good indicators of friendships amongst chimpanzees (Crockford et al., 2013; Fraser et al., 2008; Massen & Koski, 2014; Massen, Sterck, & De Vos, 2010), and therefore indicate to what extent chimpanzees choose to socialise or spend time with others.

4.2.4 Behavioural data compilation.

Data were compiled separately for focal observations, scans and all-occurrence grooming records. Compilation was done using R. All data were arranged with each observation as a separate data point.

There were a total of 6557 scan data points, for a total of 706 scans (i.e. for each scan, every individual in the scan was included on a separate row in the dataset). Each observation for each individual was labelled with date, number of observation periods for that date and scan number for each observation period.

Number of scan observations per individual ranged between 184 and 459 (mean = 345.10, *SD* = 73.83). There were 216 instances of grooming another chimpanzee, 184 instances of receiving grooming, and 90 instances of mutual grooming.

There were 731 focals for all chimpanzees, with between 33 and 45 focal observations per chimpanzee (mean = 38.47, *SD* = 2.84). Mean focal length was 7.92 minutes (*SD* = 3.10 minutes). For neighbour proximity (in meters), we removed 31 data points for which the cell was mislabelled or the distance was not clear, resulting in 700 cases of neighbour proximity. There were between 32 and 43 observations of proximity for all 19 chimpanzees (mean instances = 36.84, *SD* = 2.54).

Table 4.1

Ethogram of behaviours recorded during individual focal observations

Behaviours to be noted during focal	Notes
Neighbour proximity	Record ID and distance of nearest neighbour in a point sample at the start of the focal sampling period
Eating	Record whether focal eats, and what they eat
Regurgitating	Record if focal regurgitates; note the time, where they regurgitated (e.g. hand, mouth, floor), who else was present, their distance from focal chimp, and whether they observed the regurgitation. If other events (e.g. aggression) distract you from close observation of the focal animal so you can no longer be sure if R/R occurred or not, record N/A
Defecation	Record if focal produces faeces, quality of faeces, and whether they put it in their mouth
Length of focal	If focal leaves the observation area before 10 minutes, note total time focal lasted

Table 4.2

Ethogram for observations of all occurrence social grooming

Record	Notes
Occurrence	Note whether social grooming occurs within group during each observation period
IDs	Record ID of actor and recipient
Duration	Record start and end time; if grooming started before the observation began or ended after the observation finished, note it as incomplete
Intergroom	Record if grooming is mutual

Table 4.3

Item loadings for each chimpanzee personality component

	Item loadings	
Personality component	Negative	Positive
Dominance	Submissive	Dominant
	Dependent	Independent
	Fearful	Decisive
	Timid	Intelligent
	Cautious	Persistent
	Vulnerable	Bullying
	Anxious	Stingy
		Manipulative
Extraversion	Solitary	Active
	Lazy	Playful
	Individualistic	Social
	Depressed	Friendly
		Affectionate
		Imitative
Conscientiousness	Defiant	
	Reckless	
	Erratic	
	Irritable	
	Aggressive	
	Jealous	
	Disorganised	
	Thoughtless	
	Distractible	
	Unperceptive	
	Quitting	
Agreeableness		Sympathetic
		Helpful
		Sensitive
		Protective
		Gentle
		Conventional
Neuroticism	Stable	Excitable
	Cool	Autistic
Openness		Inquisitive
		Inventive
		Curious
		Innovative

Nearest neighbour proximity varied between 0 and 21 meters (mean = 2.28, *SD* = 0.6). For regurgitation (did the focal regurgitate? Y/N) there were 3 missing cases, and 27 instances of regurgitation for 7 of the chimpanzees (12 individuals were not observed to regurgitate). Between 1 and 9 instances of regurgitation were observed per individual (mean = 3.86, *SD* = 2.48). As there were only 6 cases of eating faeces, these data were excluded from further analyses.

A total of 591 instances of grooming were recorded for all chimpanzees. We removed 63 cases where duration was not clearly recorded, resulting in 528 data points of grooming duration. There were 587 data points for actor, with four missing cases. Instances of giving grooming ranged from 8 to 84 per chimpanzee (mean = 26.30, *SD* = 19.20). There were 589 data points for recipient, with only 2 missing cases. Instances of receiving grooming ranged from 4 to 69 per chimpanzee (mean = 26.40, *SD* = 20.22). Duration of each bout was recorded in minutes, with each bout lasting between 1 and 31 minutes (mean bout duration = 4.72, *SD* = 5.16). Sixteen bouts of grooming continued after the focal ended.

4.2.5 Analyses.

All analyses were run in R version 3.0.2 (R Core Team, 2013). Personality scores and autism scores were converted in to *z*-scores for analysis (mean = 0, *SD* = 1).

For numeric variables, including neighbour proximity and grooming duration, we ran linear mixed models using the lme4 package (Bates, Maechler, Bolker, & Walker, 2015). For grooming duration we ran separate analyses for the actor and the recipient.

For the grooming variables, social groom instances and direction of grooming, we ran generalised linear mixed models with family set to binomial, treating each behaviour as a binary category. For observations of grooming, we scored each instance of social grooming as 1, including give, receive or mutual grooming, and compared this with self-groom, scored as 0, dropping all non-grooming observations. To calculate frequency of grooming direction, we split the social grooming data into a variable where we compared give grooming, scored as 1, with receive grooming, scored as 0, and dropped all non-social groom data.

For regurgitation data, we calculated total number of instances per chimpanzee and ran a poisson regression using generalised linear models. Only seven individuals in the group showed regurgitation behaviour, and amongst them, instances varied between 1 and 9 observations. For this reason, we re-ran the model 19 times to account for the 19 subjects, in each case excluding one subject. We then took the mean of the coefficients, standard error and confidence intervals for these models.

We analysed each behaviour as a dependent variable in its own model. For the mixed models, we included all six personality components, autism scores, age and sex as fixed effects, and chimpanzee ID as a random effect. For the poisson models, we included independent variables of all six personality components, autism scores, age and sex. To avoid issues of collinearity between personality scores and autism scores, we examined personality and autism scores in separate models. For each behavioural variable, we thus ran four models. The first included autism score as a predictor. The second model included predictors of autism score, sex and age. We then compared these two models for the best model fit. The third model for each behaviour included predictors of all six personality components. The fourth and final model included personality, sex and age. We then compared the third and the fourth models for the best model fit. In each set of models for each behaviour (i.e. for the personality models and for the autism score models) we report the model with the best fit. Where we found significant effects of both autism score and personality, we use Akaike information criteria to compare model fit. We report confidence intervals calculated using the Wald method.

4.3 Results

4.3.1 Stereotypic behaviours.

Regurgitation.

For the full sample, we found a significant effect of autism score on regurgitation, and a significant effect of Neuroticism and Dominance (Table 4.4). The AIC for the autism scores model was 80.42, and the AIC for the personality model was 52.24; comparison of fit between the two models revealed that the personality model is a better fit for the data ($p < .001$). When we re-ran the model, removing each subject at a time, and then calculated the mean values of all 19 models, we found the same significant effects (Table 4.5), suggesting that our results were not affected by extreme outliers.

Table 4.4

Autism scores and personality components as predictors of regurgitation instances in the full sample

	b	*SE*	*p*
	Autism scores		
(Intercept)	0.21	0.22	.34
Autism scores	**0.67**	0.28	**.016**
	Personality		
(Intercept)	-0.64	0.44	.14
Dominance	**1.84**	0.93	**.048**
Extraversion	0.41	0.42	.34
Conscientiousness	0.53	0.33	.11
Agreeableness	-0.01	0.42	.98
Neuroticism	**2.63**	0.80	**.001**
Openness	-0.88	0.52	.090

Note. Significant findings are highlighted in bold.

Table 4.5

Autism scores and personality components as predictors of regurgitation instances in the mean model

	b	l-95%, u-95% CI	*SE*
	Autism scores		
(Intercept)	0.19	-0.32, 0.61	0.24
Autism scores	**0.68**	**0.17, 1.32**	0.29
	Personality		
(Intercept)	-0.76	-2.08, 0.05	0.52
Dominance	**2.16**	**0.11, 4.83**	1.18
Extraversion	0.40	-0.58, 1.52	0.52
Conscientiousness	0.61	-0.12, 1.45	0.39
Agreeableness	0.02	-1.01, 1.10	0.52
Neuroticism	**2.93**	**1.18, 5.40**	1.04
Openness	-1.09	-2.53, 0.04	0.64

Note. Results present mean values of 19 replications. For each model, 1 subject was excluded.

Significant findings are highlighted in bold.

Table 4.6

Effects of autism score and personality on nearest neighbour distance

	b	l-95%, u-95% CI	*SE*
	Distance to neighbour ~ autism scores		
(Intercept)	2.28	2.03, 2.55	0.14
Autism scores	-0.10	-0.40, 0.19	0.14
	Distance to neighbour ~ personality		
(Intercept)	2.37	1.22, 3.51	0.58
Dominance	0.15	-0.60, 0.89	0.38
Extraversion	-0.41	-0.88, 0.07	0.24
Conscientiousness	0.12	-0.34, 0.58	0.24
Agreeableness	0.29	-0.22, 0.80	0.26
Neuroticism	-0.02	-0.68, 0.64	0.34
Openness	0.05	-0.38, 0.47	0.22
Sex	**0.83**	**0.08, 1.58**	0.38
Age	-0.02	-0.06, 0.02	0.02

Note. Significant effects highlighted in bold.

4.3.2 Social behaviours.

Neighbour proximity.

We found no significant effects of either autism score or personality on distance to nearest neighbour, but we did find a sex effect: males tended to be further away from their nearest neighbour than females (see Table 4.6).

Grooming duration.

There was no effect of autism score or personality on grooming duration, for either actors or recipients (see Table 4.7).

Grooming instances and direction.

There was a significant positive association between autism score and instances of social grooming compared with self-grooming. That is, individuals with higher autism scores groomed with others significantly more than they groomed themselves. There were no significant associations between personality and grooming (Table 4.8).

When we examined the direction of grooming, we again found a significant effect of autism score – individuals with higher scores were more likely to receive grooming. For the personality model, Extraversion showed a significant association with giving grooming, whilst Neuroticism was significantly associated with receiving grooming (see Table 4.9). Model comparison between the models for personality and autism score revealed that personality was a significantly better fit of the data, AIC personality = 458.54, AIC autism scores = 460.52, p = .046.

4.4 Discussion

We found that chimpanzees with higher autism scores had a higher number of regurgitation instances, spent more time grooming with others than self-grooming, and received grooming more than they gave grooming. For the personality data, we found that chimpanzees higher in Neuroticism and Dominance had a higher number of regurgitation instances, whilst extraverted chimpanzees groomed others more, and chimpanzees high in Neuroticism received grooming more. For both the regurgitation data and direction of grooming data, the personality model was a better fit than the autism scores model. These results suggest that personality is a stronger predictor of social and stereotypic behaviours than the autism scale measure, supporting our second but not our first prediction.

Table 4.7

Autism scores and personality on duration of grooming bouts for actor and recipient

	b	l-95%, u-95% CI	*SE*
Duration grooming for actor ~ autism scores			
(Intercept)	4.73	4.16, 5.29	0.29
Autism scores	-0.03	-0.61, 0.54	0.29
Duration grooming for actor ~ personality			
(Intercept)	4.68	4.01, 5.35	0.34
Dominance	-0.39	-2.14, 1.36	0.89
Extraversion	0.12	-0.97, 1.20	0.55
Conscientiousness	-0.46	-1.42, 0.49	0.49
Agreeableness	0.03	-0.94, 1.01	0.50
Neuroticism	-0.65	-2.21, 0.91	0.80
Openness	0.53	-0.53, 1.59	0.54
Duration grooming for recipient ~ autism scores			
(Intercept)	4.70	4.22, 5.17	0.24
Autism scores	0.30	-0.21, 0.82	0.26
Duration grooming for recipient ~ personality			
(Intercept)	4.85	3.97, 5.73	0.45
Dominance	-0.23	-2.57, 2.10	1.19
Extraversion	-0.29	-1.52, 0.93	0.63
Conscientiousness	0.48	-0.86, 1.83	0.69
Agreeableness	-0.37	-1.73, 1.00	0.70
Neuroticism	0.06	-2.04, 2.17	1.08
Openness	0.10	-1.15, 1.34	0.64

Table 4.8

Effects of autism scores and personality on social grooming vs. self grooming

	OR	l-95%, u-95% CI	*b*	*SE*
Groom type ~ autism scores				
(Intercept)	5.52	3.68, 8.28	1.71	0.21
Autism scores	**1.55**	**1.04, 2.30**	0.44	0.20
Groom type ~ personality				
(Intercept)	5.83	3.94, 8.61	1.76	0.20
Dominance	1.17	0.50, 2.76	0.16	0.44
Extraversion	0.78	0.47, 1.30	-0.25	0.26
Conscientiousness	0.82	0.46, 1.44	-0.20	0.29
Agreeableness	1.11	0.66, 1.88	0.10	0.27
Neuroticism	1.42	0.63, 3.20	0.35	0.41
Openness	0.76	0.44, 1.29	-0.28	0.27

Note. Confidence intervals calculated based on odds ratios.
Significant effects highlighted in bold.

Table 4.9

Effects of autism scores and personality on giving grooming vs. receiving grooming

	OR	l-95%, u-95% CI	*b*	*SE*
Give grooming ~ autism scores				
(Intercept)	2.07	0.29, 14.8	0.73	1.00
Autism scores	**0.53**	**0.29, 0.97**	-0.63	0.30
Sex	2.48	0.80, 7.74	0.91	0.58
Age	0.96	0.90, 1.03	-0.04	0.03
Give grooming ~ personality				
(Intercept)	1.15	0.74, 1.77	0.14	0.22
Dominance	0.42	0.13, 1.30	-0.87	0.58
Extraversion	**4.23**	**2.08, 8.62**	1.44	0.36
Conscientiousness	1.05	0.54, 2.04	0.05	0.34
Agreeableness	0.75	0.39, 1.46	-0.29	0.34
Neuroticism	**0.36**	**0.13, 0.99**	-1.01	0.51
Openness	0.63	0.30, 1.30	-0.46	0.37

Note. Confidence intervals calculated based on odds ratios.
Significant effects highlighted in bold.

Autism score, Neuroticism and Dominance all predicted regurgitation behaviour. The finding for Dominance is somewhat surprising, particularly as negatively loading items on this component include *fearful, vulnerable* and *anxious*. It would be useful to explore this relationship further, examining whether higher ranking chimpanzees experience more stress or differences in coping mechanisms that could lead to stereotypy. Regurgitation was most strongly related with Neuroticism, which includes negatively loading items *cool* and *stable*. Notably, the HPQ item *autistic* loads positively on the Neuroticism component. This item is defined by the description 'Subject often displays repeated, continuous, and stereotyped behaviours such as rocking or self clasping'. Thus individuals who score high on this item are likely to have been observed exhibiting stereotypic behaviours. It is possible that there are separate underlying mechanisms – one for Neuroticism and one for Dominance - that both contribute to the production of stereotypic behaviours such as regurgitation. More behavioural data are needed to explore this possibility, in particular examining a wider range of stereotypic behaviours.

Our third prediction was that, should neither personality nor autism scores predict behaviours, then the immediate environment was likely a stronger influence of these behaviours than any internal variable. As we found that personality was associated with stereotypic behaviour, this suggests that to some extent the production of stereotypies are a result of internal individual differences in neurotic or dominant traits. Stereotypies are considered a means of coping with a stressful environment (Davenport & Menzel, 1963; Harlow, 1958; Kalcher-Sommersguter et al., 2013; Mason et al., 2007), suggesting that our findings reflect individual differences in coping with the environment. But we cannot rule out environment altogether as an influence on stereotypy. It is important to consider that all of the chimpanzees that were observed to regurgitate came from the Beekse Bergen group, who originated from a laboratory. This suggests that environment has played a role in the occurrence of stereotypy in our sample. However, not all of the Beekse Bergen chimpanzees were observed to regurgitate. This points us back to the idea that individual coping mechanisms in response to the environment may vary. In this study we did not measure environmental effects directly, nor did we account for the possibility that personality can be influenced by the environment during early life. That is, we tried to separate out internal effects as being independent of external effects on behaviour, but by taking this approach we were unable to account for the possible role of early-life environment in shaping personality or development (Bard et al., 2014; Suomi, 2006).

We therefore conclude, in regards to stereotypies, that in examining occurrence of stereotypies within a group, it is important to account for individual differences and underlying causes in addition to considering both current and prior environmental effects. Such effects could include rearing history (Bard et al., 2011), experience of social housing or social deprivation (Kalcher-Sommersguter et al., 2013) as well as current housing (Carlstead et al., 1999), and early life trauma, such as maternal separation (Bloomsmith, Baker, Ross & Lambeth, 2005).

We found no association between personality or autism scores with either grooming duration or proximity to nearest neighbour. These findings indicate that other variables, such as who the neighbour or grooming partner is (Massen & Koski, 2014; Morton et al., 2015) might be more important in predicting these behaviours. We did in fact find a sex effect for neighbour proximity, with females tending to be nearer to their closest neighbour than males. Although we found no personality effects for neighbour proximity, female chimpanzees are more agreeable than males (King et al., 2008), and according to the levels of agonism received are also lower ranking than males (Muller, 2002), suggesting that they may be more tolerant of conspecifics than their male counterparts.

Whilst there were no personality effects of social vs. self-grooming, we did find that autism score was a significant predictor of social grooming. This at first seems surprising, as we would expect chimpanzees with higher autism scores to groom with others less. However, when accounting for the direction of grooming, it is apparent that autism score is associated with receiving over giving grooming. Similarly, there were directional effects of grooming for personality. Extraverted chimpanzees groomed others more, whilst chimpanzees with high Neuroticism were groomed by others more. Again, comparing the models for personality and autism scores revealed that personality was a better fit of the data. Notably, Neuroticism and autism scores both share an association with regurgitation and with receiving rather than giving grooming. This suggests that autism scores may closely reflect neurotic traits, or share the same underlying mechanism in predicting these behaviours.

So why do some chimpanzees groom others more, and some receive grooming more? Extraverted chimpanzees are social, friendly and affectionate, whilst chimpanzees with high scores on Neuroticism are excitable and unstable. Thus consistent with previous findings on grooming behaviour (e.g. Crockford et al., 2013), for extraverted individuals, grooming may provide a way to maintain good relationships and interact with others. Social bonds are an important part of group life amongst primates, acting to reduce stress, provide support, and increase reproductive success and longevity (Seyfarth & Cheney, 2012). However it is possible that the individual mechanisms of such bonds vary. For neurotic individuals, grooming may serve a less social purpose and perhaps be protective against stress. One approach to understanding this could be to examine whether there are differences in grooming networks for chimpanzees with different personalities. For example, one would expect that more extraverted chimpanzees would groom with a larger network of conspecifics than introverted chimpanzees, particularly if this was their primary means of positive social interaction. On the other hand, it is more likely that neurotic chimpanzees would prefer a small, regular network of trusted individuals from whom they could seek reassurance from grooming, if indeed grooming did serve a reassuring function. Evidence in baboons indicates that it does: females decrease their grooming network during periods of stress (Wittig et al., 2008); and females with a smaller but more concentrated grooming network experience lower glucocorticoid levels than when they groom with a wider network of females (Crockford, Wittig, Whitten, Seyfarth, & Cheney, 2008).

Another possible avenue to explore in understanding personality and grooming behaviour would be to consider neuropeptide changes such as oxytocin. In chimpanzees, oxytocin levels increase following grooming with a bond partner compared to no grooming, but no such increase is found following grooming with non-bond partners (Crockford et al., 2013). It could be useful to examine to what extent changes to oxytocin following grooming differ for extraverts vs. introverts, and for neurotic vs. emotionally stable chimpanzees.

Overall, these findings suggest that when considering stereotypic and grooming behaviours, personality is a better predictor than autism scores. The autism scores themselves did not tell us much about chimpanzee behaviour that could not be explained by personality. However, this is not to say that chimpanzees are not a good model by which to understand the origin of traits associated with autism. Chimpanzees, like humans, vary in their problem solving abilities (Herrmann & Call, 2012), cognitive performance (Hopkins, Russell, & Schaeffer, 2014), recognition of emotional stimuli (Kano, Tanaka, & Tomonaga, 2008) and social interactions (Pederson et al., 2005). Furthermore, they vary in their social responsiveness, in the same way that humans do (Marrus et al., 2011). Whilst autism remains very much a human condition, the parallels in social behaviour that can be drawn between humans and nonhuman primates (Watson & Platt, 2012) suggest that some of the behaviours associated with autism are likely ancestral and predate the occurrence of autism. The reasoning behind this is thus. One of the notable characteristics of autism is that it exists on a spectrum, with individuals exhibiting a great degree of variation in cognitive abilities, social skills and behaviours (DSM-V: APA, 2013). This variation is akin to that which is observed in chimpanzee stereotypies and coping mechanisms – every individual is different (Birkett & Newton-Fisher, 2011). There are also notable similarities in the types of human and nonhuman primate behaviours that are classed as atypical. For example, repetitive motion or posturing, self-injury and self-induced vomiting have been observed both in nonhuman primates (Clay et al., 2015; Suomi & Harlow, 1972) and humans (Emerson et al., 2001; Goldman et al., 2009). Stereotypies are thought to be a coping mechanism, perhaps acting as a substitute for a behaviour that cannot be exhibited within the given environment, or providing a consequence such as relief, sensory stimulation or even pleasure (Mason, 1991; Mason & Latham, 2004). Thus, the fact that there are inter-specific similarities in behavioural coping mechanisms, and that these behaviours show great inter-individual variation, suggests that they likely predate modern humans.

The role of individual differences in assessing and understanding the variation in stereotypies and atypical social behaviours is clearly important. Personality data could therefore provide a useful approach to understanding why some chimpanzees exhibit some traits more than others. It has been suggested that the within-trait variation of personality evolved as a result of varying selection pressures in differing environments (Nettle, 2006), or as a result of frequency-dependent selection (Bouchard & Loehlin, 2001). Perhaps similar mechanisms played a role in the variation of atypical behaviours. Primates are highly social animals (Dunbar, 2013) who often live in large groups; they have knowledge of others' relationships (Seyfarth, Cheney, & Bergman, 2005), learn from each other (Whiten, 2000), cooperate and share food (Melis et al. 2010; Stanford, Wallis, Mpongo, & Goodall, 1994; Yamamoto et al. 2009), and use facial expressions and gestures to communicate emotions (Parr, Hopkins & de Waal, 1998; Visalberghi, Valenzano & Preuschoft, 2006). Within this growing social complexity, it is possible that trait extremes and atypical behaviours emerged within a continuum of social behaviours and cognitive abilities. Indeed, several findings indicate that chimpanzees vary in their social cognition (Herrmann et al., 2009; Vonk & Povinelli, 2011) and that, in several primate species including humans, traits such as higher Openness (Altschul et al., 2016; DeYoung et al., 2014; Morton, Lee, & Buchanan-Smith, 2013) and lower

Assertiveness (Morton, Lee, & Buchanan-Smith, 2013) are associated with higher cognitive performance. To understand the origins and underlying causes of atypical behaviours, we might do well to consider the role of personality in social cognition in nonhuman primates.

Our findings indicate that it is important to account for personality when considering welfare. For example, if neurotic individuals are more prone to stereotypy, this may be used as a way to predict at-risk individuals who might struggle to cope in stressful situations. This could be useful in helping those individuals adapt to new situations, or to identify group members who would be likely to adapt well if transferred to another zoo, for example for breeding purposes. Further research would benefit from examining the combined role of personality and early-life environment in resulting behaviours. We know for example that chimpanzee infants raised either with standard care or responsive care exhibit differences in social behaviour at one year old (Bard et al., 2014). Individuals in the responsive care environment, who received five times as much interaction with caregivers as standard care chimpanzees, and also experienced species-typical interactions with their caregivers, exhibited higher levels of cooperative behaviour and joint attention success than their standard care counterparts (Bard et al., 2014). Furthermore, disorganised attachment in adult chimpanzees was significantly associated with rocking behaviour (Clay et al., 2015). The same study in fact found no significant differences in personality between chimpanzees with different rearing backgrounds or different attachment types. However it did find that chimpanzees with organised attachment tended to have above-average well-being scores, which were negatively associated with abnormal (i.e. stereotypic) behaviour and stress behaviour (scratch, yawn). We thus encourage further research that explores the relationship between personality, environment and resulting welfare indicators.

Whilst these data suggest that that it is important to account for individual differences in understanding population-level behaviours, we should also be careful to note several limitations of this study. Firstly, our sample was limited to one location with a relatively small sample size. Given that differences between samples have been observed in cognition (for example in Bräuer, Call & Tomasello (2009)), it is important to examine whether similar relationships between personality and social/stereotypic behaviour occur in other chimpanzee populations too. An additional and perhaps primary concern of the current study is that we were unable to present inter-observer reliability of the behavioural data analysed. Although efforts were made in the training process to ensure that observers were accurate and consistent in their recordings of individuals and behaviours, without an inter-observer assessment we cannot conclude whether these data were quantitatively reliable between multiple observers. Finally, it is important to stress the need for more research examining the interaction of internal (genetic and neural) processes with external (physical, social) processes on behavioural outcomes. For these reasons we encourage study of behavioural individual differences in other samples.

To summarise, whilst the autism scale measure was not very revealing in this study, we did find links between personality and social and atypical behaviours. The use of personality assessment, in conjunction with assessment of environmental factors, may help us to understand the origins and variability of atypical behaviour in chimpanzees, and which individuals are more prone to these behaviours. Examining in particular traits of Dominance, Extraversion and

Neuroticism in relation to a wider group of stereotypic behaviours could help us to identify factors associated with the heterogeneous nature of stereotypies (Birkett & Newton-Fisher, 2011). For example, further exploration of the link between Neuroticism and stereotypic behaviour could be useful. It would also be interesting to examine whether similar associations exist in other species, or whether predictors of atypical behaviour patterns vary across species. The study of personality is becoming of increasing relevance to captive management, and thus personality assessments could be beneficial to improving individual welfare. Finally, understanding the links between personality and environment are key to providing social and physical environments that cater to the needs of all individuals in group-housed settings. We particularly encourage further research in this area.

Chapter 5. Individual Differences in Emotional Perception in Chimpanzees

> "*Empathy allows one to quickly and automatically relate to the emotional states of others, which is essential for the regulation of social interactions, coordinated activity, and cooperation toward shared goals*."
>
> - Frans B. M. de Waal (2008, p. 282)

5.1 From Social Interactions to Emotional Perception

In the previous chapter, results indicated that personality was a good predictor of social behaviours. In particular, we observed personality differences in the direction of social grooming in chimpanzees, that is, whilst extraverted individuals were more likely to groom others, neurotic individuals were more likely to receive grooming. At present, we can only hypothesise as to why this might be. For example, neurotic individuals may use grooming as a way to seek reassurance from others and reduce anxiety (Crockford et al., 2008). What these data do tell us is the importance of accounting for social interactions and interactional direction (e.g. who approached who, who initiated contact, etc.). Examining behavioural states alone is not enough to understand the ways in which personality is associated with social behaviours.

In this chapter, I examine emotional perception, by assessing how individuals differ in their response to emotions in others and whether personality plays a role in these differences. We know from previous research into chimpanzee post-conflict behaviour that individuals consistently differ in the extent to which they reconcile with others (Webb et al., 2014).

Furthermore, research in humans highlights the links between empathetic behaviour and personality. Studies that specifically examine the links between empathy[11] and personality are few, which is likely due to the fact that empathetic items are often included in personality measurements (Jolliffe & Farrington, 2006). For example, a measure of altruism, which can be empathy based (de Waal, 2008) is included in the assessment of Agreeableness (Costa & McCrae, 1992). Empathy may also be treated as a personality trait in itself (Brown, Sautter, Littvay, Sautter, & Bearnes, 2010; Davis, 1980; Davis et al., 1999). Thus it is perhaps not so surprising that, when measured separately, empathy correlates with some personality traits.

What is more noteworthy is that empathetic measures in humans correlate with varying personality domains, depending on what form of empathy is being measured. For example, an overall index of empathy correlates most strongly with Friendliness (Barrio, Aluja, & Garcia, 2004). Similarly, facets of affective empathy (experiencing another's emotions) and empathic concern correlate with Agreeableness (Jolliffe & Farrington, 2006; Mooradian, Davis, & Matzler, 2011). In contrast, facets of cognitive empathy and perspective taking were found to correlate with both Agreeableness and Openness (Jolliffe & Farrington, 2006; Mooradian et al., 2011). Sex specific findings also reveal that cognitive empathy was positively correlated with Conscientiousness in males, whilst

---

[11] I use empathy here to refer to questionnaire based assessments of empathy, which primarily address emotional and cognitive empathy, as well as related facets such as personal distress and fantasy.

affective empathy was positively correlated with Conscientiousness and Openness among males but with Neuroticism among females (Jolliffe & Farrington, 2006). In addition to examining empathic concern and perspective taking, Mooradian et al. (2011) also examined relationships for two other facets of empathy. They found that personal distress (a facet of the Interpersonal Reactivity Index (IRI) (Davis, 1980) that describes dealing with emotionally difficult situations) and fantasy (a facet of the IRI that describes emotional involvement and imagination about fictional scenarios) were most strongly related to Neuroticism and Openness, respectively. The latter relationship is perhaps unsurprising given that fantasy is a facet of Openness (Costa & McCrae, 1992). However such a finding highlights the importance of examining personality traits in relation to different aspects of empathetic behaviours, such as emotional contagion versus cognitive empathy.

One way to help understand individual differences in empathetic behaviour is to examine whether personality relates to emotional perception in nonhuman primates. This approach allows us to consider the evolutionary origins of personality traits that may play a role in empathy, particularly if we address this question in chimpanzees, with whom we share a very similar personality structure (King & Figueredo, 1997; Weiss et al., 2009).

5.2 Assessing Emotional Perception in Chimpanzees

In this chapter, I examine individual differences in response to conspecifics' emotions in captive chimpanzees, thus using response as a way to measure perception. This chapter has three components. First, we observed chimpanzees in their group and recorded how individuals responded to emotion in conspecifics. Second, we assessed chimpanzees' response to video footage of emotional stimuli. Third, we examined associations between responses in these different contexts to see if chimpanzees respond to emotional stimuli consistently across contexts.

5.3 Part 1: Behavioural observations

In the wild, chimpanzees live in large groups which form and divide by fission-fusion (Aureli et al., 2008; Lehmann & Boesch, 2004), a process whereby large groups break into smaller groups and smaller groups merge into larger groups. Such a dynamic may be beneficial to reducing resource competition (Lehmann & Boesch, 2004). Chimpanzees are prone to conflict, and it has been suggested that, due to the social instability that comes with their changing group dynamics, male chimpanzees must constantly reassert their dominance to maintain their social status (Muller, 2002).

Chimpanzees use 'display' behaviour to intimidate others, which may result in aggression (Coe & Levin, 1980). Displays are usually a routine of loud behaviours which attract attention and cause disturbance amongst group members. Behaviours usually involve a combination of pant-hoot vocalisations, drumming hands and feet on loud surfaces, swaying the body from side to side, bipedal swaying, throwing objects, and charging at/chasing others (Nishida, Kano, Goodall, McGrew, & Nakamura, 1999). Goodall (2000: 112-114) described a situation at Gombe where a low ranking male chimpanzee, who was challenging for alpha position, used metal kerosene cans in his charging displays. The noise and motion of the cans, directed at a group of grooming males, caused the other males to rush out of the way, achieving the displaying individual's desired effect of getting everyone's attention.

Although display behaviours are strongly linked to conflict, they are not necessarily directed at particular individuals (Coe & Levin, 1980) and may also occur as a result of excitement or arousal. At Edinburgh Zoo, feeding time or the opening of the outdoor enclosure often leads to displays as chimpanzees anticipate these events. As colleagues and I have observed, one low ranking male chimpanzee, in response to displays or conflict, often runs into an empty part of the enclosure and displays out of sight of his conspecifics, thus releasing his own arousal without attracting attention from other males.

Because both conflict and displays involve the exhibition of emotion, I used these events as a way to measure response to emotion in conspecifics. During a period of pilot observations at Edinburgh Zoo, I noted that not all chimpanzees responded every time there was a display or fight, and those that responded did so in different ways. Thus, I decided to record whether, and how, chimpanzees responded to events of conflict and display. Returning to my discussion of emotional perception in Chapter 1, I defined five levels of emotional perception. These were: 1) emotional contagion/arousal, 2) emotional awareness/recognition, 3) sympathy, 4) emotional empathy and 5) cognitive empathy. Previous research indicates evidence of the first three of these in chimpanzees (see Chapter 1). I thus used behavioural observations to examine individual differences in these three[12] levels of behaviours in chimpanzees.

I used response (do they respond?) as a measure of emotional awareness of each event. I should note here that I worked on two assumptions: firstly, that

---

[12] Emotional and cognitive empathy will be addressed in the next section of the chapter

emotional awareness is necessary to recognise emotions, and secondly, that chimpanzees do recognise emotions (given previous findings, e.g. Morimura & Matsuzawa, 2001; Parr, 2001). Thus I did not directly measure emotional recognition, but instead focused on responsiveness to emotional states. In each case that a chimpanzee responded, I used type of response (e.g., Are they aroused? Do they show state matching?) as a measure of emotional contagion and arousal to each event, as well as an additional measure of awareness (e.g. do they direct attention towards the event?). By gathering information on different response types, I chose to examine whether these behaviours would group into the above levels as expected given the conceptual definitions, rather than defining response categories based on the conceptual levels. Finally, I measured sympathetic behaviour by observing instances of reassurance of individuals who had received aggression. The purpose of these observations was to examine if and how individuals differed in their responses to emotion, and whether differences could be explained by personality.

Given that people show individual differences in empathetic traits that are linked to personality (Baron-Cohen & Wheelwright, 2004; Davis, 1980; Barrio et al., 2004; Jolliffe & Farrington, 2006; Mooradian et al., 2011), we expected to find similar results in chimpanzees. Based on these findings, we predicted that (1) individual chimpanzees will consistently differ in whether and how they respond to emotion in conspecifics; (2) chimpanzees that score higher on sociable factors - Agreeableness and Extraversion - are likely to be more responsive to emotions in others than chimpanzees with low scores; (3) extraverted chimpanzees are more likely to exhibit arousal and contagion in response to emotional events; and (4) chimpanzees that score highly on

Agreeableness will offer consolation to conspecifics following conflict more frequently.

5.4 Methods

5.4.1 Subjects.

Observational data were collected for 18 adult chimpanzees housed at the Budongo Trail facility in Edinburgh Zoo (see Chapter 4 for more details). When testing began, the group consisted of 10 females and 8 males, between 15 and 50 years old (mean age = 27.22, *SD* = 11.68) (Table 5.1).

5.4.2. Behavioural data.

Event types.

Event types and types of response were determined through pilot observations at Edinburgh Zoo, which took place between 26 June and 12 July 2013. I noted that occurrence of conflict and displays could occur independently, but could also overlap with each other, and with related behaviours. For example, a display from one chimpanzee could be met with a crescendo of hoots from another, or with submissive pant grunts towards the chimpanzee that displayed. I thus recorded responses to all of these events (see Ethogram in Table 5.2). Behavioural definitions were determined through pilot observation, with guidance from Bloomsmith, Lambeth, & Alford (1990), Coe and Levin (1980), Nishida et al. (1999), and Schel et al. (2013).

Behavioural observations were conducted with a camcorder using focal sampling (Altmann, 1974). This required following and recording one focal animal for thirty minutes. All observations lasted for thirty minutes, with the exception of five cases where the focal was cut short due to technical problems with the camera. Abbreviated observations were between 11 minutes 50 seconds and 26 minutes 49 seconds long. All chimpanzees were observed once a week for twelve weeks, with the exception of two chimpanzees: PE, who was observed in week 13 instead of week 12. And LU, who received an extra focal in week 13 due to an error in the observations record. Between two and seven individuals were observed on any one day, over three or four days per week. The order of observation for each week was pre-determined through randomised selection, to ensure that each chimpanzee was observed at different times of day and on different days. In any case where a chimpanzee could not be found to be observed (for example if they were in the off-show area), they were observed at the next available opportunity.

Data collection took place for an initial eight week period between 13 January and 21 March 2014, and for a second four week period between 22 September and 21 October 2014. The four week period of observation was timed to coincide with experimental data collection (see 5.7). Between these periods female HL gave birth to an infant. As much as possible, observations were counterbalanced across morning and afternoon sessions to ensure that there was minimum biased from time of day (such as feeding time, rest time). Dates and times of data collection are noted in Table C2, Appendix C.

Events were recorded on all-occurrence basis. During each focal, when a conflict, display or related event occurred, the time and description of the event were noted. When events were sequential (e.g. LB displays; PA then displays; LB then chases PA) each of these would be recorded as a separate event. In the case where a chimpanzee displayed and then, mid display, chased or initiated conflict with another chimpanzee, this was recorded as one event. If more than one individual was involved in the event, for example, KD and PA display at the same time or LI gives submissive pant grunts as PA hoots, this was treated as one event.

Response to events.

As each event occurred, response of the focal chimpanzee was recorded. First, it was noted whether the focal individual did respond. Then their type of response was recorded. As a range of behaviours could be exhibited in response to these events, I decided to record all types of response. The assembled ethogram thus resulted in 18 categories of response type which were determined during pilot observations (Table 5.2). There was an additional category, 'other' to record any other behaviours not listed. Behaviours were all categorical, namely, I recorded whether they did or did not take place. This with the exception of three categories, in which additional levels were indicated: 'Move' specified direction of movement; and both 'Vocalisation' and 'Facial expression' specified type of vocalisation/expression (see Table 5.2). If the focal chimpanzee was out of sight when an event took place, this was also noted.

Sympathetic behaviours.

In addition to recording immediate response to events, I recorded instances of sympathetic behaviour in the chimpanzees. There were four categories: the first was to record if the focal individual showed consolation behaviour to another chimpanzee after a fight between conspecifics.

The second category recorded if consolation was offered to the focal if they were involved in a fight. The third and fourth category recorded if the focal offered support or intervention during a fight.

Table 5.1

Sex and date of birth for all 18 adult chimpanzees that were observed

Chimpanzee ID	Sex	DOB	Video study
CI	F	01/01/1964	P^+
DA	M	02/03/1975	P
ED	F	11/04/1996	P^+
EM	F	15/08/1981	P^+
EV	F	09/12/1980	P^+
FK	M	21/10/1993	P^+
HL	F	16/04/1991	P
KL	F	20/02/1993	P^+
KD	M	05/02/1997	P
LI	F	14/02/1989	---
LB	M	20/01/1999	P^+
LO	M	01/01/1976	P^+
LU	F	11/11/1976	---
PA	M	08/05/1993	P
PE	F	13/03/1969	P^+
Q	M	31/03/1992	P
RE	M	21/02/1993	P^+
SO	F	22/11/1981	P

Note. Video study refers to the second section of this chapter (see 5.7).
P = participated. $^+$ = completed testing.

If any of these behaviours were observed, further information was recorded if observed for any of 12 other variables. These included names of individuals involved and details of behaviours such as embracing, kissing, grooming (see Table 5.2).

5.4.3 Video coding.

I conducted all behavioural observations. An independent coder who was blind to the predictions of this study coded all the videos for events and behaviours. This was done to reduce coding biased that could result from my own expectations about the chimpanzees' behaviour. The independent coder coded all videos as assessing interrater reliability using this method would be impractical due to the heavy time constraints of coding. The coder had previous experience observing both wild and captive chimpanzees, and was familiar with all of the Edinburgh chimpanzees. The second coder was provided with training on how to code the videos, and before beginning coding completed behavioural coding of four practice focals which I checked to ensure they were consistent with the ethogram and coding method. Video playback was run in VLC and all coding was done in Microsoft Excel.

Coding consisted of noting when an event occurred, the nature and description of the event, who was involved (if it was known) and how the focal individual responded. Because the nature of the events meant a certain degree of variation in the exhibited behaviours, descriptions of the events were recorded during coding and later categorised. In some instances, poor lighting/visibility or noise from visitors meant that it was difficult to determine behaviours or vocalisations. The coder was instructed to only code behaviour that was clear. Where the nature of the event, individuals involved or response of the focal were unclear or unknown, this was noted.

5.4.4 Personality data.

We had personality data for all 18 chimpanzees. Personality ratings were collected prior to this study, in 2010 (Herrelko et al., 2012). Although personality traits do vary with age, personality ratings tend to show good test-retest reliability (Freeman & Gosling, 2010). As such, we took the ratings for these chimpanzees to still be valid measures of individual variation. Data were collected using the HPQ (Weiss et al., 2009), which is described in Chapter 2. Each chimpanzee was rated by between two and four raters (mean = 3.0, *SD* =

1.03). We assessed interrater reliability using the same method described in Chapter 2. We found three items to be unreliable (less than or equal to 0) – these included *impulsive, predictable* and *clumsy*. Components were scored using the structure in Weiss et al. (2009) (see Chapter 4, Table 4.3), the only difference being that we excluding the unreliable items. This produced six components, labelled Dominance, Extraversion, Conscientiousness, Agreeableness, Neuroticism and Openness. We calculated mean score per individual and standardised all six variables using *z*-scores for analysis.

5.4.5 Analyses.

All analyses were run in R version 3.0.2 (R Core Team, 2013). Data from all focal observations were included in the analyses, with two exceptions: one focal from chimpanzee CI had in error not been coded, and a second focal from PA was removed due to errors in the time stamps. This resulted in a total of 215 observations, for a total of 6,399 minutes and 47 seconds.

Event type.

We used event descriptions from the video coding to determine event types. We separated descriptions of events into five categories, including Conflict, Displays, Display and Conflict together, Hoots, and Other (see Table 5.2: responses listed in the middle two columns could occur in response to any of the five event types in the two left hand columns). The Other category included primarily submissive pant grunts, which can indicate dominance rank (who is being submissive to whom) (Nishida et al., 1999), and one instance of waa-barks, which have been observed in response to conflict (Slocombe & Zuberbühler, 2005) but also in response to danger (Schel, Townsend, Machanda, Zuberbühler,

& Slocombe, 2013), suggesting that the meaning of these calls may be context-dependent. Descriptions of categories are included in Table C1 in Appendix C. In instances where descriptions could fit into more than one category (for example 'Hoots/submissive barks') the description was included in the predominant category (see note in Table C1, Appendix C). We removed 5 data points from the events variable due to errors or unclear information. We removed another 45 data points as at the time of recording, the nature of the event was not clear.

Proportion response.

We collected responses to a total of 208 instances of Conflict, 460 instances of Displays, 59 instances of Display and Conflict together, 461 instances of Hoots, and 61 instances of Other. All events were observed for all focal individuals, except in four cases: two chimpanzees (ED and Q) did not have any instances of Display and Conflict during their focal observations, and two chimpanzees (EM and LB) did not have any instances of Other events.

We recorded 726 Yes responses (focal chimpanzee responds) and 278 No responses (focal chimpanzee does not respond) to all events. On 249 occasions, the focal individual was out of sight when the event occurred. We removed 46 instances where it was not clear whether the focal responded.

To examine differences in response, we first calculated each chimpanzee's proportion of response, to (1) all events [frequency of responses per chimpanzee/total number of all events per chimpanzee], and (2) to each event [frequency of responses per chimpanzee per event type/total number of each event type per chimp]. This allowed us to examine whether any general patterns of responsiveness (i.e. to all events) were consistent with responsiveness at each event level. As data were proportions and therefore not linear, in each model we used an arcsine transformation on both measures (Viechtbauer, 2010).

We first examined proportions of responses to all events using linear models. With proportion response as the dependent variable, in the first model we included all six personality variables as predictors. In the second model we added predictors of age and sex. We then compared model fit, choosing the model with the smallest residual sum of squares, i.e., the model that best balanced fit and parsimony.

We then examined proportion of response to each event type using linear mixed models to examine effects across event category per chimpanzee. We included proportion response as the dependent variable and chimpanzee as a random effect, to account for response per event type (i.e. for each chimpanzee, there was one data point per event type, so five data points per chimpanzee). In the first model we included all six personality variables as predictors. In the second model we added predictors of age and sex. We then chose the model with the smallest Akaike Information Criteria (AIC), i.e., the best model fit.

Finally, we ran five pairs of linear models examining proportion of response to each event type, split into separate responses for Displays, Conflict, Display and Conflict, Hoots, and Other. For the first model in each pair, we included all six personality variables as predictors. For the second model in each pair, we added predictors of age and sex. We then compared model fit, choosing the model with the smallest residual sum of squares as the best fit model.

For each pair of linear and linear mixed models, we report the model of best fit. For each reported model we also generated bootstrapped 95% confidence intervals for 500 samples.

Response behaviours.

We collected data on a broad range of behaviours. This allowed us to examine which behaviours grouped together as particular response types, so we could assess which behaviours were most likely to fit each level of emotional perception.

Response behaviours were all categorical. That is, whether each behaviour occurred in each case was noted, and where necessary, the direction of behaviour (e.g. Move: away or towards) or specifics (e.g. Vocalisation: screams) were noted. This allowed us to gather detailed response information. Of the 18 response categories, we examined frequency of occurrence, and for analysis retained only the behaviours with a frequency that was higher than the number of subjects. We treated each response variable as a binary factor (1 = occurred, 0 = did not occur). Using generalised linear models with behaviour as the dependent variable and chimpanzee as the predictor variable, we extracted the residuals for each behaviour. Using the residuals we then determined the number of components to extract using a parallel analysis and by inspecting the scree plot. We ran a principal components analysis (PCA) using both oblique (promax) and orthogonal (varimax) rotation. If the promax rotation did not reveal high inter-component correlations, we interpreted the components from the varimax rotation.

We scored up behavioural categories into the components determined from the PCA. We treated each component as binary, that is, in each case that a chimpanzee exhibited a behaviour that loaded on that component, they received a score of 1. In each case that none of the behaviours on that component occurred, they received a score of 0. We made an exception for one variable, which instead of having all positive or negatively loading behaviours, had one positive and one negatively loading behaviour. As one behaviour occurred in much higher frequency than the other, we retained only this behaviour, scoring this as 1 in all cases that it occurred.

We did not aggregate data, thus we had one score for each individual for each event. To examine individual differences in response behaviours for all events, we ran generalised linear mixed models using the glmer function (Bates et al., 2015), treating each behavioural component as our binary dependent variable (family = binomial, link = 'logit'), all six personality components as independent variables and chimpanzee as a random variable. For each behaviour, we ran two models – one with personality only as predictors and one including variables of age and sex. We compared model fit for each model pair (one with age and sex, one without), by choosing the model with the smallest residual sum of squares as the best fit model. We then ran variants of this model, with data subset by event type for Conflict, Display and Hoots. We excluded models for events Display and Conflict as well as Other, as the frequencies of behaviours for these events were very low. For each model we generated confidence intervals using the Wald method.

Sympathetic behaviours.

Due to the very low frequency of sympathetic behaviours, we did not analyse these data. There was one instance of the focal individual showing consolation behaviour to another chimpanzee after a fight, and one instance of consolation being offered to the focal after they were involved in a fight. There was one instance of the focal offering support, and one of them offering intervention during a fight.

Table 5.2

Ethogram of emotional events and behavioural responses to emotional events, as well as sympathetic behaviours

Events		Responses to events: assessing levels 1 and 2 of emotional perception		Sympathetic behaviours: assessing level 3 of emotional perception	
Event type	Description	Response type	Description	Response type	Description
Display	Loud show of strength; usually starts with soft hoots, tapping hands and feet on loud surfaces, swaying the body from side to side; can build to bipedal swaying, erection of body hair, a crescendo of hoots and a charge that may involve throwing objects, chasing others and drumming loudly on noisy surfaces.	Does focal individual respond?	If focal individual shows any kind of response to event, note Yes, and record which behaviours from the list below. If focal individual does not move, glance, vocalise or appear to acknowledge the event in any other way, note No.	Does focal show consolation behaviour after a fight between conspecifics?	For each of these categories, note if Yes, record which behaviours from the list below.
		If fight, does focal join in?	Does focal get directly involved with a fight between two or more conspecifics, for example by chasing one of those chimpanzees or by	Is consolation offered to focal individual after a fight?	

	providing support through presence and vocalisations: If they do, note Yes.	
Response type: 1,2	*Description*	*Response type: 3*
Look towards event	Focal turns head and directs gaze towards the individual(s) involved/location of the event.	Does focal offer support during a fight?
Look around	Focal turns head in different directions, moving gaze from one point to another around the enclosure, not focusing on any one point.	Does focal provide intervention during a fight?

Response type: 1,2	*Description*	*Response type: 3*	*Description*
Facial expression	Facial expression of focal changes in response to event. This could include: drawing back lips and showing teeth and gums in fear; looking relaxed with lips	Consolation offered to winner or loser?	Note the names of the aggressor, the victim, and who was consoled.

			slightly apart and lower lip hanging loose.		
		Response type: 1,2	*Description*	*Response type: 3*	*Description*
		Move	Focal may get up from a sitting or lying position and start walking, climbing or running through enclosure. If the direction is clearly towards or away from the event, this should be noted.	Approaches	Focal moves intentionally towards and within physical contact of an individual involved in the fight.

Event type	*Description*	*Response type: 1,2*	*Description*	*Response type: 3*	*Description*
Conflict	Aggression directed from one chimpanzee to one or more other individuals, which can involve	Piloerection	Focal's hair stands on end, giving them the appearance of being larger and hairier than normal.	Approached by	A conspecific involved in a fight moves towards and within physical contact of the focal individual.
	chasing, hitting, biting, cornering and beating the victim. The victim	Vocalisation	Focal may vocalise to events, including pant hoots – loud 'hoo' calls which are usually	Facial expression	Facial expression of focal changes in response to conspecific. They

may respond by running away, hiding, screaming, fear grinning and urinating.		uttered repeatedly, may build in volume and can be heard over long distances; screams – very loud, shrill repeated screams that are often accompanied by bared teeth displays; or pant grunts, submissive, throaty barks directed towards a more dominant individual.		will likely show an affiliative expression with mouth open and lower lip hanging down.
	Response type: 1,2	*Description*	*Response type: 3*	*Description*
	Sway	Sitting down or standing on all fours, focal starts to move slowly from side to side. Their body will form a steady rocking motion and they may also sweep their arms around them on the floor. Often accompanied by hooting and hair	Hold out hand	Focal reaches hand towards the other chimpanzee in an affiliative gesture.

			standing on end.		
		Response type: 1,2	*Description*	*Response type: 3*	*Description*
		Bipedal sway	As above but standing up on two legs and swaying, they may do this while holding and swaying a rope at the same time.	Kiss	Lips are slightly pouted and pressed to the face or body of the other chimp.
		Bipedal stand/bipedal move	Focal stands on two legs and may swagger or walk a short distance before returning to all fours.	Embrace	Will put one or both arms around conspecific and hold them tightly; may be accompanied by fear grinning or vocalisations.
Event type	*Description*	*Response type: 1,2*	*Description*	*Response type: 3*	*Description*
Display & Conflict	A combination of the above two events, which may start with one individual displaying and then chasing or attacking another	Banging/drumming	Focal uses hands and/or feet to hit a loud object such as door or wall, producing a loud clanging or drumming sound which may increase in intensity	Other	Note other behaviours involved, including behaviour directed from the consolee to the consoler.

chimpanzee, or chasing someone and then going on to immediately display without pause. It can also include display and conflict taking place at the same time.		and volume and crescendo; may be accompanied by hooting and often seen before a charging display; it may also break off abruptly with no additional behaviour.		
	Response type: 1,2	*Description*	*Response type: 3*	*Description*
	Urinating	Specifically when an individual is chased or fleeing display or conflict between others, they may urinate suddenly; often accompanied by screaming or fear grinning.	Touch	Focal reaches out hand and gently touches conspecific.
	Bob	Head moves up and down and whole body may also bob up and down, flexing the elbows; directed towards another	Allogroom	Focal begins to groom conspecific by sitting or standing next to them and using their fingers and/or

	chimpanzee; may be accompanied by pant grunts; indicates affiliative or submissive behaviour.		mouth to remove foreign objects from their hair.
Response type: 1,2	*Description*	*Response type: 3*	*Description*
Crouch bob	Similar to the bob but usually indicates submission; the individual adopts a crouching position where they are low to the ground and direct their bob to a more dominant individual; may be accompanied by fear grin or pant grunts/screams.	Play	Focal may adopt a relaxed open mouth expression (bottom lip hanging down) and utter soft grunts; they may tickle or playfully chase a conspecific, slap the ground or roll around together, or run up and down and play ‘tag’ by grabbing the other individual.
Arm wave	A brief threatening gesture. Arm is raised above the head and usually directed	Vocalise	Focal may vocalise towards conspecific, such as emitting

			towards another chimp; can sometimes form part of a display.		submissive pant grunts, play grunts or hoots. Note type of vocalisation.
Event type	*Description*	*Response type: 1,2*	*Description*	*Response type: 3*	*Description*
Hoots	Vocalisations with a 'hoo' sound. There may be several short sharp hoots, or they may start off soft and build gradually; can be accompanied by gentle swaying, but do not build to form a full display.	Full display	As described in event type. Focal may respond to a display or conflict by displaying themselves. This usually includes a crescendo of hoots followed by drumming and a charge; the charge and drumming may be very brief; the display may be accompanied by other behaviours listed in the Display event category.	Length of contact	If focal embraces or touches conspecific, note length of physical contact.
		Approaches another chimpanzee	Focal moves intentionally towards another or several chimpanzee(s) during event; this does not		

	include passing by other chimpanzees. They will pause by the intended individual, and may sit with them, groom them, inspect them (if the conspecific is a female) or offer submission in the form of crouching, pant grunts and mouthing the other.
Response type: 1,2	*Description*
Approached by another chimpanzee	As above, but from another individual directed towards the focal.
Other	List any other behaviours seen in response to events that are not listed here.

Event type	*Description*
Other	Pant grunts/barks: Deep throaty ‘barks’ indicating submission, directed from one chimpanzee towards a more dominant chimpanzee, often whilst approaching/being approached by them. Often following a display or directed aggression. Waa-bark: Loud, abrupt call that starts with a low ‘w’ and ends in a higher ‘aow’ sound.

5.5 Results

5.5.1 Proportion response.

On average there were 7.65 (*SD* = 6.40) emotional events per chimpanzee per observation day, with up to 210 minutes of observations per day. Across the group, chimpanzees responded to 62.61% of Displays; 59.32% of Displays and Conflict; 56.25% of Conflict; 49.2% of Other events; and 48.16% of Hoots.

Proportion of response across all events, regardless of event type, showed no significant association with any of the personality variables, age or sex (Table 5.3).

Proportion of response calculated per event type showed a negative association with Openness of borderline significance (Table 5.4).

Proportion of response to Displays revealed a positive, borderline association with Conscientiousness. Proportion of response to Other events revealed a significant positive association with Extraversion and a negative association with Dominance, Agreeableness and Neuroticism. We found no significant results for proportion of response to Hoots, Conflict only, or to instances of Display and Conflict (Table 5.5).

5.5.2 Response behaviours.

We retained 9 behaviours with a frequency > 18 (see Table 5.6). A parallel analysis and scree plot suggested extraction of four components. The extracted components are in Table 5.7. The promax solution revealed that components correlations did not exceed .26 (Table 5.8), thus we interpreted the varimax solution. We labelled the components Move, Interact, Look, and Arousal.

Table 5.3

Personality, age and sex as predictors of mean proportion response to all events in a linear model

	b	l-95%, u-95% CI	*SE*	*p*
Intercept	1.10	0.83, 1.36	0.12	< .001
Dom	0.02	-0.14, 0.18	0.07	.80
Ext	0.01	-0.09, 0.11	0.04	.77
Con	0.04	-0.06, 0.14	0.04	.43
Agr	0.00	-0.11, 0.11	0.05	.97
Neu	0.04	-0.11, 0.20	0.07	.52
Opn	-0.03	-0.12, 0.06	0.04	.41
Sex	0.01	-0.15, 0.17	0.07	.89
Age	0.00	-0.01, 0.01	0.00	.81

Note. Dom = Dominance, Ext = Extraversion, Con = Conscientiousness, Agr = Agreeableness, Neu = Neuroticism, Opn = Openness.

Table 5.4

Personality components as predictors of mean proportion response to each event type, for all events

	b	l-95%, u-95% CI	*SE*
Intercept	1.04	0.96, 1.11	0.04
Dom	-0.01	-0.19, 0.21	0.10
Ext	0.06	-0.04, 0.16	0.05
Con	0.12	-0.01, 0.25	0.06
Agr	-0.02	-0.15, 0.10	0.06
Neu	0.06	-0.11, 0.24	0.10
Opn	**-0.14**	**-0.24, -0.02**	0.06

Note. Dom = Dominance, Ext = Extraversion, Con = Conscientiousness, Agr = Agreeableness,
Neu = Neuroticism, Opn = Openness.
Significant effects highlighted in bold.

Table 5.5

Personality, age and sex as predictors of mean proportion response to each event type

	b	l-95%, u-95% CI	*SE*	*p*
		Conflict		
Intercept	1.02	0.44, 1.60	0.25	.003
Dom	0.12	-0.24, 0.47	0.16	.47
Ext	-0.01	-0.23, 0.20	0.09	.91
Con	0.08	-0.13, 0.30	0.10	.40
Agr	-0.01	-0.25, 0.23	0.11	.93
Neu	0.15	-0.17, 0.48	0.14	.31
Opn	-0.03	-0.22, 0.17	0.09	.74
Sex	0.17	-0.19, 0.52	0.16	.31
Age	0.00	-0.02, 0.02	0.01	.97
		Display		
Intercept	1.24	0.54, 1.94	0.31	.003
Dom	0.08	-0.35, 0.51	0.19	.68
Ext	0.05	-0.21, 0.31	0.11	.70
Con	0.26	0.00, 0.52	0.12	.052
Agr	-0.07	-0.36, 0.22	0.13	.61
Neu	0.19	-0.21, 0.58	0.17	.32
Opn	0.00	-0.24, 0.23	0.10	.98
Sex	-0.13	-0.55, 0.30	0.19	.52
Age	-0.01	-0.03, 0.02	0.01	.57
		Display and Conflict		
Intercept	1.01	-0.29, 2.30	0.55	.11
Dom	0.40	-0.37, 1.17	0.33	.26
Ext	0.04	-0.43, 0.51	0.20	.85
Con	0.14	-0.39, 0.66	0.22	.56
Agr	0.20	-0.35, 0.74	0.23	.42
Neu	0.36	-0.37, 1.09	0.31	.28
Opn	-0.25	-0.69, 0.19	0.19	.22
Sex	-0.41	-1.22, 0.41	0.34	.28
Age	0.01	-0.03, 0.05	0.02	.68
		Hoots		
Intercept	0.91	0.55, 1.27	0.16	< .001
Dom	-0.02	-0.24, 0.20	0.10	.87
Ext	-0.02	-0.15, 0.12	0.06	.77
Con	0.01	-0.13, 0.14	0.06	.93
Agr	0.02	-0.13, 0.17	0.07	.75
Neu	0.03	-0.18, 0.23	0.09	.77

Opn	0.00	-0.13, 0.12	0.05	.94
Sex	0.07	-0.15, 0.29	0.10	.51
Age	0.00	-0.01, 0.01	0.00	.80

	b	l-95%, u-95% CI	*SE*	*p*
		Other		
Intercept	0.62	-0.53, 1.77	0.49	.24
Dom	**-0.93**	-1.61, -0.25	0.29	**.015**
Ext	**0.59**	0.28, 0.91	0.13	**.003**
Con	0.06	-0.24, 0.35	0.12	.67
Agr	**-0.64**	-1.28, -0.01	0.27	**.048**
Neu	**-0.56**	-1.01, -0.10	0.19	**.023**
Opn	-0.32	-0.65, 0.00	0.14	.050
Sex	-0.09	-0.82, 0.64	0.31	.77
Age	0.01	-0.02, 0.05	0.01	.30

Note. Dom = Dominance, Ext = Extraversion, Con = Conscientiousness, Agr = Agreeableness,
Neu = Neuroticism, Opn = Openness.
Significant effects highlighted in bold.

Table 5.6

Frequency of response behaviours to all events and each event type

Behaviour	Instances				
	All*	Conf	Disp	Disp/Conf	Hoots	Other
Look towards	529[503]	91	197	26	165	24
Look around	133[127]	28	57	6	32	4
Move away	169[160]	31	79	12	35	3
Move towards	118[114]	23	32	8	44	7
Hoots	70[68]	5	27	4	32	0
Approach	24[24]	8	2	6	8	0
Approached by	24[23]	3	11	3	6	0
Sway	33[31]	5	16	0	10	0
Piloerection	21[19]	3	9	1	6	0

Note. All = all event types, Conf = Conflict, Disp = Display, Disp/Conf = Display & Conflict.
*Values outside of brackets indicate total instances observed; values inside brackets indicate total instances after removing ambiguous events.

Table 5.7

Principal components analysis of response behaviours using promax (top) and varimax (bottom) rotation

	Move	Interact	Look	Arousal	h^2
		Promax rotation			
Move away	**0.86**	0.00	0.08	-0.20	0.74
Move towards	**0.82**	-0.20	-0.04	0.17	0.69
Approach by	-0.28	**0.80**	0.04	-0.11	0.60
Approach	0.18	**0.56**	-0.05	0.03	0.40
Piloerection	0.09	**0.51**	0.01	0.05	0.31
Look towards	-0.30	-0.05	**-0.81**	0.06	0.74
Look around	-0.25	-0.02	**0.79**	0.12	0.70
Sway	-0.08	-0.15	0.06	**0.82**	0.65
Hoots	0.08	0.23	-0.04	**0.62**	0.52
		Varimax rotation			
Move away	**0.83**	0.16	0.07	-0.15	0.74
Move towards	**0.80**	-0.01	-0.05	0.20	0.69
Approach by	-0.24	**0.73**	0.06	-0.07	0.60
Approach	0.20	**0.59**	-0.05	0.08	0.40
Piloerection	0.12	**0.53**	0.02	0.09	0.31
Look towards	-0.28	-0.09	**-0.80**	0.05	0.74
Look around	-0.24	-0.07	**0.79**	0.09	0.70
Sway	-0.05	-0.09	0.06	**0.80**	0.65
Hoots	0.12	0.32	-0.04	**0.63**	0.52

Note. h^2 = communalities.
Salient loadings |> 0.4| are highlighted in bold.

Table 5.8

Component correlations determined by principal components analysis using promax rotation

	Interact	Look	Arousal
Move	.26	-.03	.12
Interact	---	.00	.18
Look	---	---	-.02

The component Look had two loading variables - 'look towards' and 'look around' - which were inversely related. Whilst both behaviours could occur in response to one event (mean instances of occurring together = 3.37, *SD* = 2.14), the behavior 'look towards' occurred nearly four times as often as 'look around' (mean instances of look towards occurring independently of 'look around' = 24.47, *SD* = 11.49) (see Table 5.6); thus we chose to include only the more frequent behavior, 'look toward', to make a binary variable (look = 1, not look = 0). We chose not to analyse 'look around' separately due to the low occurrence of look around behavior occurring independently of 'look toward' (max instances per individual = 8, mean = 3.63, *SD* = 2.11).

For the overall models, we found that adding age and sex improved the model fit in all cases, so we report these results in the tables.

Move. In the overall model, males were more likely than females to move in response to an event. In the Conflict model, Openness and Neuroticism were positively and negatively related to move behaviour, respectively. There were no significant effects for Displays or Hoots (Table 5.9).

Look. We examined only effects of look towards behaviour. In the overall model Neuroticism was positively associated with looking towards the event, and females were more likely to look than males. In the Conflict model, we found the same sex effect. We also found that age was negatively associated with looking towards Conflict events. Contrastingly, in the Display model, age was positively associated with looking towards Display events. Agreeableness was negatively associated with looking behaviour for Displays. There were no significant effects of personality, age or sex for the Hoots model (Table 5.10).

Interact. There were no significant effects of personality, age or sex for the Interact variable in any of the models (Table 5.11).

Arousal. In the overall model, Dominance, Agreeableness and Neuroticism were all positively associated with Arousal, and age was negatively associated with Arousal. There were no significant effects in the other models (Table 5.12).

Table 5.9

Personality, age and sex as predictors of Move behaviour, separated into response to all events, and Display, Conflict and Hoots only

	OR	l-95%, u-95% CI	*b*	*SE*	*p*
		Overall			
Intercept	0.73	0.37, 1.46	-0.31	0.35	.37
Dom	0.87	0.56, 1.33	-0.14	0.22	.51
Ext	0.83	0.64, 1.08	-0.18	0.13	.17
Con	0.93	0.71, 1.23	-0.07	0.14	.61
Agr	1.02	0.75, 1.38	0.02	0.16	.92
Neu	0.80	0.55, 1.18	-0.22	0.19	.26
Opn	1.09	0.86, 1.38	0.08	0.12	.48
Sex	**1.68**	1.09, 2.59	0.52	0.22	**.019**
Age	0.99	0.97, 1.01	-0.01	0.01	.35
		Display			
Intercept	0.65	0.21, 2.02	-0.44	0.58	.45
Dom	0.79	0.40, 1.56	-0.23	0.35	.50
Ext	1.08	0.72, 1.64	0.08	0.21	.71
Con	0.95	0.58, 1.53	-0.06	0.25	.82
Agr	0.86	0.54, 1.36	-0.15	0.23	.51
Neu	0.70	0.37, 1.34	-0.35	0.33	.28
Opn	0.93	0.61, 1.43	-0.07	0.22	.75
Sex	1.82	0.92, 3.61	0.60	0.35	.087

Age	0.99	0.96, 1.03	-0.01	0.02	.68
	OR	l-95%, u-95% CI	*b*	*SE*	*p*
		Conflict			
Intercept	3.94	0.43, 36.14	1.37	1.13	.23
Dom	0.28	0.07, 1.08	-1.26	0.68	.066
Ext	0.54	0.24, 1.21	-0.62	0.41	.13
Con	0.51	0.22, 1.18	-0.67	0.43	.12
Agr	1.97	0.85, 4.56	0.68	0.43	.12
Neu	**0.14**	0.03, 0.57	-1.96	0.71	**.006**
Opn	**2.23**	1.15, 4.32	0.80	0.34	**.018**
Sex	1.41	0.42, 4.77	0.34	0.62	.58
Age	0.94	0.88, 1.01	-0.06	0.03	.077
		Hoots			
Intercept	0.68	0.18, 2.54	-0.39	0.67	.56
Dom	0.95	0.41, 2.23	-0.05	0.44	.91
Ext	0.85	0.50, 1.42	-0.17	0.26	.53
Con	0.83	0.51, 1.36	-0.18	0.25	.46
Agr	1.17	0.62, 2.20	0.15	0.32	.64
Neu	1.06	0.53, 2.09	0.05	0.35	.87
Opn	1.05	0.67, 1.66	0.05	0.23	.82
Sex	1.18	0.49, 2.83	0.16	0.45	.72
Age	0.99	0.95, 1.03	-0.01	0.02	.64

Note. Dom = Dominance, Ext = Extraversion, Con = Conscientiousness, Agr = Agreeableness, Neu = Neuroticism, Opn = Openness.
Significant effects highlighted in bold.

The component Arousal included responses *sway* and *hoot*. In Chapter 1, I categorised arousal behaviour with emotional contagion, as contagion typically involves emotional arousal to match the emotional state of a conspecific. To examine whether Arousal indicated state matching in this case, we ran three additional models to test whether Arousal was significantly associated with event type. We created three new binary variables, specifying whether the event was (1) Display or not, (2) Conflict or not, and (3) Hoots or not. We excluded events Display and Conflict as well as Other due to the low frequency of Arousal responses to these events. We ran three generalised linear models, with Arousal as the dependent variable and fixed effects of either Display, Conflict or Hoots. We included chimpanzee ID as a random effect, and generated 95% confidence intervals using the Wald method. Arousal was not significantly associated with Conflict, OR = 0.56, *SE* = 0.36, *p* = .11, 95% CIs [0.28, 1.13], or Display, OR = 1.11, *SE* = 0.23, *p* = .65, 95% CIs [0.70, 1.74], or Hoots, OR = 1.54, *SE* = 0.24, *p* = .068, 95% CIs [0.97, 2.43], indicating that arousal behaviours (sway, hoot) did not occur significantly more in response to Hoots from conspecifics compared with Conflict or Display.

Table 5.10

Personality, age and sex as predictors of Look behaviour, separated into response to all events, and Display, Conflict and Hoots only

	OR	l-95%, u-95% CI	*b*	*SE*	*p*
		Overall			
Intercept	2.95	1.39, 6.25	1.08	0.38	.005
Dom	1.33	0.82, 2.18	0.29	0.25	.25
Ext	0.98	0.72, 1.33	-0.02	0.16	.90
Con	1.26	0.93, 1.71	0.23	0.16	.13
Agr	0.74	0.53, 1.04	-0.29	0.17	.083
Neu	**1.58**	1.02, 2.43	0.45	0.22	**.040**
Opn	0.97	0.74, 1.27	-0.03	0.14	.83
Sex	**0.45**	0.28, 0.73	-0.79	0.25	**.001**
Age	1.01	0.99, 1.03	0.01	0.01	.39
		Display			
Intercept	0.82	0.25, 2.68	-0.20	0.60	.74
Dom	1.45	0.69, 3.02	0.37	0.38	.33
Ext	0.90	0.56, 1.45	-0.11	0.24	.67
Con	1.45	0.87, 2.42	0.37	0.26	.16
Agr	**0.55**	0.34, 0.87	-0.61	0.24	**.011**
Neu	1.75	0.88, 3.48	0.56	0.35	.11

Opn	1.13	0.70, 1.81	0.12	0.24	.61
Sex	0.54	0.26, 1.12	-0.62	0.37	.10
Age	**1.04**	1.01, 1.08	0.04	0.02	**.022**
	OR	l-95%, u-95% CI	*b*	*SE*	*p*
		Conflict			
Intercept	96.95	6.30, 1491.12	4.57	1.39	.001
Dom	2.13	0.50, 9.04	0.75	0.74	.31
Ext	0.84	0.36, 1.96	-0.17	0.43	.69
Con	1.13	0.45, 2.87	0.13	0.47	.79
Agr	1.87	0.60, 5.85	0.63	0.58	.28
Neu	1.81	0.39, 8.35	0.60	0.78	.44
Opn	0.72	0.34, 1.51	-0.34	0.38	.38
Sex	**0.22**	0.05, 0.99	-1.51	0.77	**.049**
Age	**0.92**	0.85, 0.99	-0.08	0.04	**.031**
		Hoots			
Intercept	1.84	0.45, 7.55	0.61	0.72	.40
Dom	0.88	0.33, 2.30	-0.13	0.49	.79
Ext	0.95	0.49, 1.81	-0.06	0.33	.87
Con	1.12	0.66, 1.88	0.11	0.27	.68
Agr	0.66	0.33, 1.30	-0.42	0.35	.23
Neu	1.50	0.69, 3.28	0.41	0.40	.31
Opn	1.27	0.74, 2.20	0.24	0.28	.38
Sex	0.54	0.21, 1.39	-0.62	0.49	.20
Age	1.03	0.98, 1.07	0.03	0.02	.24

Note. Dom = Dominance, Ext = Extraversion, Con = Conscientiousness, Agr = Agreeableness, Neu = Neuroticism, Opn = Openness.
Significant effects highlighted in bold.

Table 5.11

Personality, age and sex as predictors of Interact behaviour, separated into response to all events, and Display, Conflict and Hoots only

	OR	l-95%, u-95% CI	*b*	*SE*	*p*
		Overall			
Intercept	0.09	0.03, 0.33	-2.38	0.65	< .001
Dom	0.47	0.20, 1.08	-0.76	0.42	.074
Ext	1.59	0.97, 2.59	0.46	0.25	.063
Con	1.42	0.86, 2.34	0.35	0.26	.17
Agr	1.10	0.66, 1.83	0.09	0.26	.73
Neu	0.78	0.39, 1.55	-0.25	0.35	.48

Opn	1.12	0.73, 1.72	0.11	0.22	.60
Sex	2.13	0.92, 4.95	0.76	0.43	.078
Age	0.98	0.94, 1.01	-0.02	0.02	.21
	OR	l-95%, u-95% CI	*b*	*SE*	*p*
		Display			
Intercept	0.06	0.01, 0.58	-2.85	1.17	.015
Dom	0.30	0.07, 1.27	-1.21	0.74	.10
Ext	2.01	0.90, 4.51	0.70	0.41	.089
Con	2.15	0.78, 5.95	0.77	0.52	.14
Agr	0.99	0.44, 2.25	-0.01	0.42	.98
Neu	0.73	0.22, 2.48	-0.31	0.62	.62
Opn	1.33	0.62, 2.85	0.29	0.39	.46
Sex	2.27	0.50, 10.37	0.82	0.78	.29
Age	0.97	0.91, 1.04	-0.03	0.04	.45
		Conflict			
Intercept	0.76	0.04, 14.52	-0.27	1.51	.86
Dom	0.45	0.07, 2.78	-0.79	0.92	.39
Ext	0.74	0.16, 3.38	-0.31	0.78	.69
Con	1.04	0.28, 3.84	0.04	0.67	.95
Agr	1.62	0.49, 5.35	0.48	0.61	.43
Neu	0.53	0.11, 2.64	-0.63	0.82	.44
Opn	1.87	0.65, 5.40	0.63	0.54	.25
Sex	2.29	0.27, 19.34	0.83	1.09	.45
Age	0.91	0.82, 1.01	-0.10	0.05	.072
		Hoots			
Intercept	1.03	0.02, 53.77	0.03	2.02	.99
Dom	0.40	0.06, 2.96	-0.91	1.02	.37
Ext	2.89	0.61, 13.73	1.06	0.79	.18
Con	1.16	0.52, 2.60	0.15	0.41	.72
Agr	1.72	0.52, 5.74	0.55	0.61	.38
Neu	0.60	0.13, 2.76	-0.51	0.78	.51
Opn	0.39	0.09, 1.73	-0.94	0.76	.22
Sex	1.09	0.10, 11.83	0.09	1.22	.94
Age	0.89	0.78, 1.03	-0.11	0.07	.11

Note. Dom = Dominance, Ext = Extraversion, Con = Conscientiousness, Agr = Agreeableness,
Neu = Neuroticism, Opn = Openness.
Significant effects highlighted in bold.

Table 5.12

Personality, age and sex as predictors of Arousal behaviour, separated into response to all events, and Display, Conflict and Hoots only

	OR	l-95%, u-95% CI	*b*	*SE*	*p*
		Overall			
Intercept	0.42	0.14, 1.28	-0.86	0.56	.13
Dom	**3.17**	1.50, 6.67	1.15	0.38	**.00**
Ext	0.75	0.47, 1.19	-0.29	0.24	.22
Con	0.80	0.54, 1.20	-0.22	0.20	.29
Agr	**2.10**	1.38, 3.19	0.74	0.21	**.00**
Neu	**2.19**	1.14, 4.22	0.78	0.33	**.02**
Opn	0.92	0.63, 1.35	-0.08	0.20	.67
Sex	0.97	0.50, 1.85	-0.04	0.33	.91
Age	**0.96**	0.93, 0.99	-0.04	0.02	**.02**
		Display			
Intercept	0.06	0.01, 0.58	-2.85	1.17	.02
Dom	0.30	0.07, 1.27	-1.21	0.74	.10
Ext	2.01	0.90, 4.51	0.70	0.41	.09
Con	2.15	0.78, 5.95	0.77	0.52	.14
Agr	0.99	0.44, 2.25	-0.01	0.42	.98
Neu	0.73	0.22, 2.48	-0.31	0.62	.62
Opn	1.33	0.62, 2.85	0.29	0.39	.46
Sex	2.27	0.50, 10.37	0.82	0.78	.29
Age	0.97	0.91, 1.04	-0.03	0.04	.45
		Conflict			
Intercept	0.76	0.04, 14.52	-0.27	1.51	.86
Dom	0.45	0.07, 2.78	-0.79	0.92	.39
Ext	0.74	0.16, 3.38	-0.31	0.78	.69
Con	1.04	0.28, 3.84	0.04	0.67	.95
Agr	1.62	0.49, 5.35	0.48	0.61	.43
Neu	0.53	0.11, 2.64	-0.63	0.82	.44
Opn	1.87	0.65, 5.40	0.63	0.54	.25
Sex	2.29	0.27, 19.34	0.83	1.09	.45
Age	0.91	0.82, 1.01	-0.10	0.05	.07
		Hoots			
Intercept	1.03	0.02, 53.77	0.03	2.02	.99
Dom	0.40	0.06, 2.96	-0.91	1.02	.37
Ext	2.89	0.61, 13.73	1.06	0.79	.18
Con	1.16	0.52, 2.60	0.15	0.41	.72
Agr	1.72	0.52, 5.74	0.55	0.61	.38

	OR	l-95%, u-95% CI	*b*	*SE*	*p*
Neu	0.60	0.13, 2.76	-0.51	0.78	.51
Opn	0.39	0.09, 1.73	-0.94	0.76	.22
Sex	1.09	0.10, 11.83	0.09	1.22	.94
Age	0.89	0.78, 1.03	-0.11	0.07	.11

Note. Dom = Dominance, Ext = Extraversion, Con = Conscientiousness, Agr = Agreeableness,
Neu = Neuroticism, Opn = Openness.
Significant effects highlighted in bold.

5.6 Discussion

We found that personality is associated with responsiveness in chimpanzees, supporting our prediction that individual chimpanzees consistently differ in whether and how they respond to emotion in conspecifics. Chimpanzees who were low in Openness were the most responsive to emotional events in conspecifics, a finding that we did not predict. We found no significant relationship between Agreeableness or Extraversion and level of overall responsiveness. Openness in chimpanzees is defined by the traits *inquisitive* and *curious*. Whilst this finding suggests that an individual's response to events in others is not related to their sociability, the negative correlation with Openness is curious as it suggests that overall responsiveness is not related to curiosity or interest in others. Pederson et al. (2005) found that Openness in chimpanzees was negatively associated with being idle. Openness has also been associated with research participation (Herrelko et al., 2012). These findings suggest that chimpanzees high in Openness are active and engaged with their environment, but perhaps, they are less engaged with the social aspects of their environment.

For Displays, conscientious chimpanzees were the most responsive, although this effect was only close to significance. Conscientiousness is defined by negatively loading items such as *reckless* and *erratic*, *thoughtless* and *unperceptive*. This suggests that responsiveness to displays is not necessarily an automatic process but perhaps a considered response, such as monitoring and being aware of others' action. This fits with our definition of responsiveness, that is, the awareness of emotions in others. The possibility of different levels of emotional processing in chimpanzees is also consistent with findings for different types of empathetic processes in humans (Kanske, Böckler, Trautwein, & Singer, 2015; Moore, Dev, Jeste, Dziobek, & Eyler, 2015).

For events designated Other, we found that extraverted individuals and those low in Dominance, Neuroticism and Agreeableness responded the most. These events included primarily submissive pant grunts. Submissive pant grunts can indicate dominance rank (who is being submissive to whom) (Nishida et al., 1999). Previous research shows that group living primates know the social rank of their conspecifics (Seyfarth, Cheney & Bergman, 2005). It thus makes sense that chimpanzees should pay attention to submissive pant grunts to obtain knowledge of dominance hierarchy. Individuals low in Dominance were more likely to respond to these events, suggesting that knowledge of the dominance hierarchy is more important to low-ranking chimpanzees. This is consistent with findings in patas monkeys (*Erythrocebus patas*) where lower ranking individuals direct attention to higher ranking individuals more than vice versa (McNelis & Boatright-Horowitz, 1998).

For Other events, extraverted individuals were more responsive, in line with our predictions, yet contrastingly agreeable chimpanzees were less responsive. Agreeableness includes positive loadings of *sensitive, gentle* and *sympathetic*, traits that one would expect to be associated with an empathetic response. This suggests that a response to submissive pant grunts is not indicative of empathy. It is interesting that this is the only event for which Extraversion predicts responsiveness. That is, extraverted chimpanzees are only more responsive than introverted chimpanzees when the event contains information directly relevant to the dominance hierarchy (Nishida et al., 1999). This suggests that responsiveness is not dependent on sociability, unless an event has information of important social value. Finally, why would low Neuroticism be associated with responses to submissive pant grunts? Chimpanzees low in Neuroticism are described by traits *cool, calm* and *unemotional*. Perhaps, if responsiveness is an attention-based process rather than an automatic one indicating arousal or emotional contagion, then chimpanzees who are not easily aroused are more likely to monitor socially important events in conspecifics. Exploring our behavioural results should allow a better understanding of what behaviours constitute responsiveness, and if personality is strongly related to any particular behavioural responses.

Our behavioural findings indicated that, whilst personality was clearly a predictor of response to events, the relationship was not as straightforward as we expected. Counter to our prediction, we found no effect of Extraversion on response behaviours. This supports the above suggestion that responsiveness is more indicative of interest in or attention to others, rather than how sociable an individual is. There was also no association of Conscientiousness with response behaviours.

Agreeableness was found to have a positive association with Arousal in response to all events, and a negative association with Look behaviour for display events. Similarly, Neuroticism was positively associated with Look behaviour towards all events, and negatively associated with Move behaviour in response to conflict. Examining the promax rotation for these components shows that Look is slightly, inversely related to both Move and Arousal, indicating that a chimpanzee can either become aroused (sway, vocalise) and move in response to an event, or look towards it, but is not likely to do both. Previous research has suggested that looking behaviour is a measure of social attention (Kano & Tomonaga 2010; McNelis & Boatright-Horowitz, 1998; Seyfarth, Cheney & Bergman, 2005; von Rohr, van Schaik, Kissling, & Burkart, 2015). Thus it seems likely that here, looking towards an event serves the same purpose, and is thus best considered as a measure of emotional awareness which, consistent with theoretical definitions (e.g. de Waal, 2008) operates somewhat[13] independently of emotional arousal.

Move behaviour in response to Conflict was positively associated with Openness, suggesting that individuals move because they are curious about the conflict. Finally, Dominance and Neuroticism were positively associated with Arousal to all events, a component defined by behaviours *sway* and *hoot*. As display behaviour forms part of chimpanzees' behavioural repertoire when trying to assert their dominance (Muller, 2002), it makes sense that Dominance predicts behaviours

---

[13] I use the word 'somewhat' here, as the reader will recall from Chapter 1, whilst different levels of emotional processing and response occur, these responses are still part of a layering system (de Waal, 2008) which implies that they cannot be entirely independent.

often associated with display. Chimpanzees high in Neuroticism are excitable and emotional, which fits with them being more easily aroused.

The fourth behavioural component that we explored was Interact – defined by approach behaviours and piloerection. This component was not significantly associated with any personality components. The fact that Interact behaviours occur in response to events independently of personality suggests that these behaviours may be related to other variables, such as the identity of conspecifics – i.e. the chimpanzees involved in a conflict or nearby neighbour. It would be worth examining this in future.

In addition to personality differences, we found several age and sex effects of responsiveness. Males were more likely than females to move in response to all events, whereas females were more likely than males to look towards all events. Females also looked more than males in response to conflict events. These responses fit with sex differences in the social hierarchy. Male chimpanzees are dominant to females and exhibit high aggression levels, meaning females are often the victims of male aggression (Muller, 2002). Thus as males rival for alpha position they should be more likely to show interest and involvement in conflict, whereas females should pay attention to where the conflict is and try to avoid it.

The results suggest that response to events changes with age. Age was negatively associated with looking towards Conflict events, and positively associated with looking towards Display events. Such directional differences are surprising, given that conflict and display behaviours are closely connected (Coe & Levin, 1980). It makes sense that as individuals age they lose interest in hierarchy-related agonism as it is likely of less relevance than to a younger chimpanzee who still has opportunity to climb the social ranks. It is possible that age-related changes in response to conflict reflect individual level of involvement in conflict in general. For example, in human females, age is negatively related to aggressive behaviour, which is mediated by decreasing testosterone levels (Dabbs & Hargrove, 1997). It is possible that similar mechanisms take place in chimpanzees, and it would be worth exploring individual agonism rate in relation to how individuals respond to conflict in conspecifics. It is however difficult to explain why older age would be associated with looking more towards Displays, but not Conflict. It is possible that age could mediate rank-related effects, which we did not assess. Age seems to play a role in chimpanzee rank, for example, female dominance rank increases with age (Pusey, Williams, & Goodall, 1997). Further exploration of age and rank in relation to response to agonistic content would be useful to establish whether this is a chance finding.

5.7 Part 2: Experimental

The second part of this study used experimental stimuli to examine whether chimpanzees have ‘social expectations’. Previous work has found that chimpanzees respond to video footage in a similar way to humans. Chimpanzees have comparable vision and colour perception to humans (Jacobs, 1993; Matsuzawa, 1985) and share similar flicker-fusion thresholds, suggesting that they perceive moving images in a similar way that we do (D’eath, 1998). Evidence from responses to videos supports this. For example, chimpanzees show similar looking patterns to humans in response to digital images: when shown images of chimpanzees, humans and another mammal, chimpanzees and humans both look consistently longer at the face than any other body region, and longer at the body than any background information (Kano & Tomonaga, 2009). Chimpanzees can also learn a problem solving task by watching a video of a chimpanzee solving the task (Hopper, Lambeth, & Schapiro, 2012). They are thus able to attend to and follow video footage of chimpanzees as they would live animals. They can also recognise emotional stimuli from video footage (Kano et al., 2008), which appears to be independent of the effects of luminance, colour and change between frames (Kano & Tomonaga, 2010). Furthermore, they can discriminate footage of different emotional valence (Morimura & Matsuzawa, 2001). Taken together, these findings suggest that video footage is a suitable stimulus for assessing chimpanzee social expectations.

In the behavioural part of this study we assessed responses to conflict-related events within the group. We examined responses at the first two levels of perception, that is, emotional arousal and emotional awareness. For the experimental part of the study, I used footage of non-familiar chimpanzees involved in conflict. I aimed to use videos to test chimpanzees' capacity for empathy (levels 4 and 5). As there has been much discussion as to whether chimpanzees can understand the emotional perspective of conspecifics (see Chapter 1) I focused on the assessment of cognitive empathy for this part of the study. By assessing social expectations using video footage, I aimed to examine in more detail whether chimpanzees understand emotional perspectives.

To experimentally assess social expectations to emotions first requires a measure that can test response to video footage. Studies of emotional perception have varied from assessments of behavioural observations including consolation and helping behaviour (de Waal & Aureli, 1996; Fraser et al., 2008; Melis et al., 2010; Yamamoto et al., 2009), expression recognition and responses on video and touch screen tasks (Morimura & Matsuzawa, 2001; Parr, 2001; Parr, Hopkins, & de Waal, 1998), to measures of gaze (Kano & Tomonaga 2010; von Rohr et al., 2015) and physiological measures such as temperature and heart rate changes (Berntson et al., 1989; Parr & Hopkins, 2000).

Explicit responses to social stimuli can be measured using forced choice tasks, such as the match-to-sample method (Overman & Doty, 1980), which allows us to test whether individuals can associate two separate stimuli above chance, such as matching emotional expressions of different individuals (Parr, Hopkins, & de Waal, 1998). The limitation of this approach is that it requires time to train animals to understand this task, and individuals must be willing to continue to participate on a regular basis. Physiological measures provide useful information about arousal (Berntson et al., 1989; Parr & Hopkins, 2000), but cannot tell us much about perceptions of emotional situations. An alternative approach to measuring responses to social stimuli is to use implicit measures such as looking time. Experiments using looking time usually require minimal or one-off participation, which is ideal for individuals that are cautious of participating. It is also a time and resource efficient method for collecting data.

Looking time is primarily a measure of attention (Peltola, Leppänen, Palokangas, & Hietanen, 2008) but it can also be used as an indicator of preference or interest, such as looking longer at novel over familiar faces (Gothard, Brooks, & Peterson, 2009). Chimpanzees appear to be particularly interested in agonistic video footage (Kano & Tomonaga, 2010). They also look longer at scenes of infanticide than scenes of hunting, aggression or neutral behaviours (von Rohr et al., 2015). von Rohr et al. (2015) suggest that this response is a result of their social expectations (i.e. how an adult chimpanzee behaves towards an infant) being violated. In this case, looking time provides a suitable measure of social expectations in response to social stimuli. For example, a scenario with an unexpected outcome should violate expectations and result in more attention being directed to such an outcome than a scenario with a predictable outcome. For this study, I chose looking time as my dependent variable.

I assessed social expectations using a social scenario. Participants first saw a conflict scene, repeated three times, followed by either an ‘expected’ or ‘unexpected’ outcome. The expected outcome showed an emotional response, the unexpected outcome showed an unemotional response. I predicted that (1) If participants engage with video content and recognise the scenario after first view, they should habituate to the footage and show decreased looking time in the second and third viewings. (2) If participants grasp the scenario, the surprise value of the “unexpected” outcome should make them look longer at the screen. If they do not, they should look longer at the “expected” outcome, as emotional stimuli elicit longer looking times (Kano & Tomonaga, 2010). (3) Given links between cognitive empathy and Openness in humans (Jolliffe & Farrington, 2006; Mooradian et al., 2011), and associations of Openness with cognitive performance in primates (Altschul, Terrace, & Weiss, 2016; Lee, & Buchanan-Smith, Brosnan, et al., 2013), I expected that chimpanzees with high Openness scores (curious, inquisitive) would be more likely to differentiate between the social outcomes.

5.8 Methods

5.8.1 Participants.

We used the same chimpanzees as in section 5.4. Sixteen of the chimpanzees participated in the experiments. Ten of these completed testing (see Table 5.1).

5.8.2 Ethics.

All research complied with Home Office regulations and was approved by the University of Edinburgh Animal Welfare and Ethical Review Body.

5.8.3 Stimuli.

I collected video footage of chimpanzees from Chester Zoo. The collection of footage was approved by Chester Zoo's Ethical Review Committee. All footage was collected from 1–14 August 2014. None of the participating chimpanzees were familiar with the Chester Zoo group. Clips of specific chimpanzees were edited together using iMovie to form each scenario. Care was taken to ensure that separate clips were continuous in their background features. Screen shots from the scenario can be seen in Figure 5.2.

5.8.4 Set-up.

I collected all experimental data, with the assistance of keepers. A pilot study took place on two separate days, three months prior to data collection. This involved showing the chimpanzees short clips of video footage of chimpanzees (this footage was different to the experimental clips). The pilot study allowed me to test the chimpanzees' interest in, and responses to the video footage. From these sessions the keepers and I concluded that participants were interested in the footage and importantly, did not appear to be distressed or react aggressively towards footage of conflict.

The experimental study took place between the 18 September and 17 October 2014. Research was conducted daily in designated testing times between 09:00 and 10:30 on Mondays, Tuesdays, Thursdays and Fridays. The chimpanzees were tested between one and four days per week. Testing took place both in the indoor research rooms and at the outdoor research station. The indoor research rooms consisted of two conjoined rooms with four stations where chimpanzees could take part in experiments. The outdoor research station allowed chimpanzees to view and respond to stimuli through a Perspex screen between their outdoor enclosure and the outdoor research room. The set up is shown in Figure 5.1.

A monitor and speakers were placed at one station in front of the Perspex window. The monitor was placed on a box so it was level with the window, and was connected to a computer from where I could select which videos the chimpanzees saw. One camcorder was placed either side of the screen to record testing.

Chimpanzees could sit in front of the screen to participate. The chimpanzees were not trained to be separated, so most of the testing took place with other individuals present. As some chimpanzees were reluctant to participate in the presence of more dominant individuals, when necessary, a keeper would distract certain individuals with a juice reward to allow others to participate. Individuals that did not want to approach the screen were allowed to participate from further away, as long as they could see and hear the video.

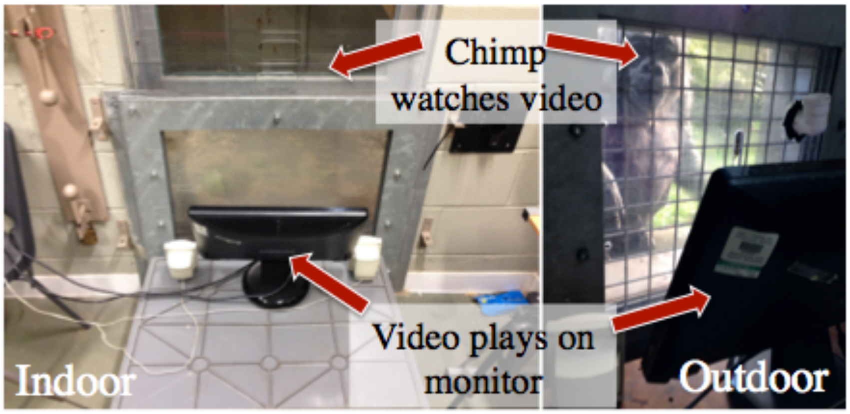


Figure 5.1

The set up for the experimental study, for the indoor research room (left) and outdoor research room (right). From the research room, chimpanzees could view the video footage on the monitor that was placed behind a Perspex window.

Participation was voluntary and the chimpanzees were free to leave at any time. In the indoor research rooms participation was rewarded with juice which could be poured through a tube in the wall. This tube was not available in the outdoor research room, so participation was rewarded with frozen juice cubes which could be pushed through a slot in the window. Prior to testing, a food from the chimpanzees' daily diet was scattered in the indoor research rooms. This encouraged individuals to come into the rooms and participate in testing.

Testing at the outdoor research station began after testing indoors was completed. As the outdoor station offered research participation in an open space, it allowed testing of some individuals who were reserved about entering the indoor research rooms.

5.8.5 Procedure.

We presented participants with two scenarios, one shorter than the other (see Figure 5.2). The shorter scenario was 30 seconds long. The longer scenario was 56 seconds long. Both scenarios depicted conflict, showing an alpha male chase a sub-adult male. Participants watched each scenario on loop three times, which allowed them to get acquainted with the footage, and allowed us to test whether they showed recognition of the video content with repeated viewings. After viewing the loop three times, they then saw an outcome to the scenario. As the outcome footage was novel, we expected looking time to increase relative to looking time to the third scenario loop. We presented two outcomes, one emotional, one unemotional, both depicting the victim of the conflict. For the shorter scenario, the emotional outcome was 22 seconds long and the unemotional outcome was 13 seconds long. For the longer scenario, the emotional outcome was 13 seconds long and the unemotional outcome was 11 seconds long. The chimpanzees saw both outcomes, counterbalanced across participants for order of presentation.

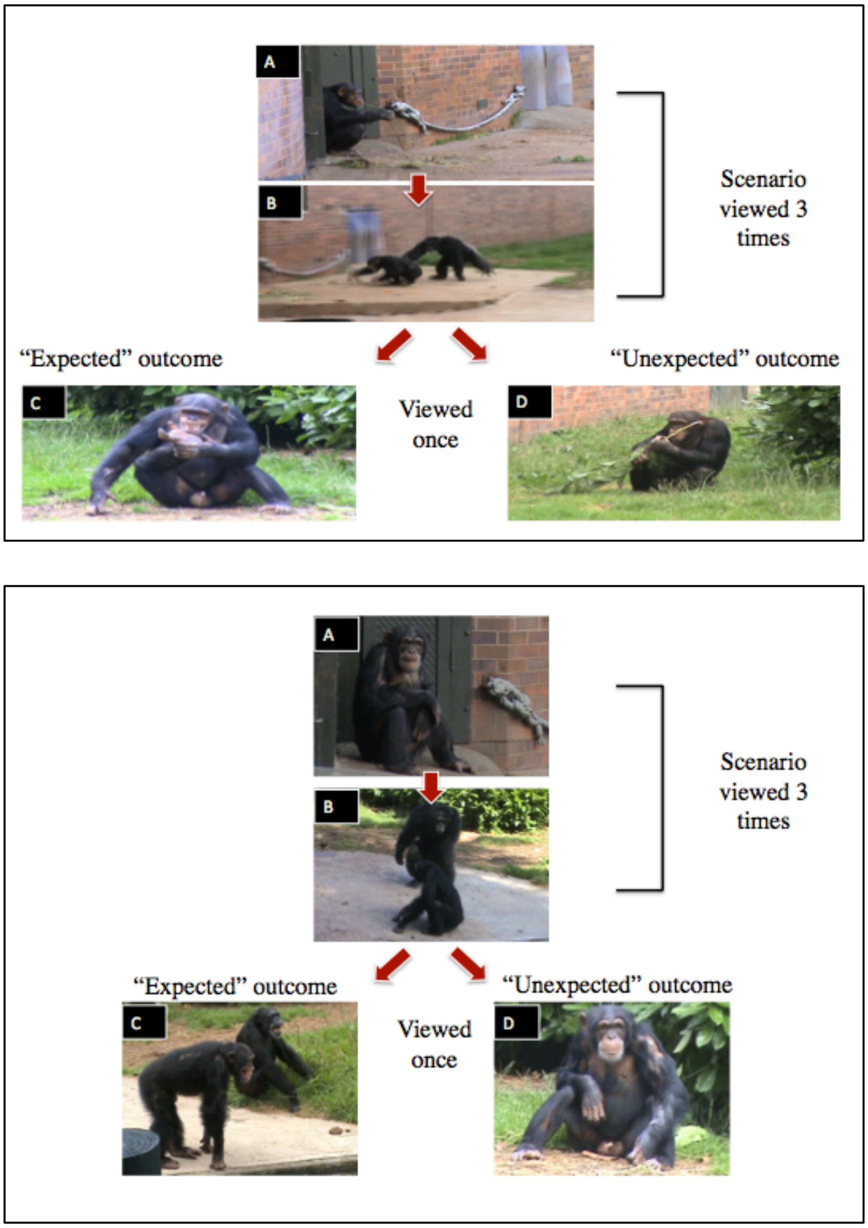


Figure 5.2

Description of social scenarios. Top: Shorter scenario. Bottom: longer scenario. A. Both scenarios first introduce a subadult male, who is at first sitting calmly; he becomes the ‘victim’ in each scenario. Scene B shows the subadult male as the recipient of aggression from the alpha male, who chases and hits the subadult male in both scenarios. Scenes A – B form the scenario, which the chimpanzees watch three times in a loop. They are then presented with either outcome C or outcome D. In outcome C the victim of the fight is screaming and fear grinning. In outcome D the victim appears calm and unemotional. Between each scene there is a short fade to black.

We ordered the scenarios, so all chimpanzees first saw the shorter scenario and outcomes. If after viewing the shorter scenario they still wished to participate, we showed them the longer scenario. All responses were video recorded.

In some instances individuals would leave half way through watching a loop. If this happened, the video was paused and the individual encouraged to return. If they did not return, they would watch the clip again another time, starting from the beginning.

Control.

To control for the presence and brightness of the screen, we ran a control condition in which the chimpanzees were required to sit in front of the screen for 60 seconds. The screen was lit but remained blank. We encouraged chimpanzees to stay for the full 60 seconds by giving them juice rewards. If they left before the 60 seconds were up, we did not repeat the condition.

5.8.6 Coding.

We used looking time as a measure of attention. We measured looking time by coding from video recordings how long each chimpanzee looked at the screen while the video was playing. We excluded looking time to the screen when each clip faded to black. I coded all videos, and to assess interrater reliability a second independent coder who was blind to the hypotheses of the study coded 50% of all the videos, selected at random. As length of scenarios and outcomes differed, we used proportion looking time as our dependent variable.

5.8.7 Analyses.

Inter-coder reliability.

We first examined inter-coder reliabilities for raw looking time using Spearman's rank correlations, as looking time was skewed towards 0. We examined correlations of looking time scores between coders for the blank condition, for each loop of the scenario, and for all outcomes grouped together. We also examined whether there were mean differences in looking time between coders for each condition, using a Wilcoxon signed-rank test.

Control condition.

To examine differences in looking time between the blank screen and video conditions, we calculated mean per chimpanzee of proportion looking time to loop 1 for both scenarios. We then ran a paired *t*-test comparing mean proportion looking time to loop 1 with proportion looking time to the blank condition. We used an arcsine transformation on the proportion data to meet assumptions of linearity.

Experimental conditions.

To compare differences in looking time between the outcomes, we ran a linear mixed model using the lmer function (Bates et al., 2015), with arcsine transformed proportion looking time as the dependent variable, chimpanzee ID as a random variable, and fixed effects of scenario type, outcome type, and scenario x outcome interaction. We generated 95% confidence intervals using bias-corrected and accelerated bootstrapping for 500 samples.

To examine effects of personality on looking time to each outcome, we ran a linear mixed model with arcsine transformed proportion looking time as the dependent variable, chimpanzee as a random variable, and fixed effects of outcome type and all six personality variables. We then ran the same model, but included age and sex as fixed effects. We compared model fit using AIC and report the model with best fit. Finally, to determine whether the relationship between personality and looking time differed between the emotional and unemotional outcomes, we ran an additional model examining interaction of significant personality predictor variables with outcome type.

5.9 Results

All 16 participants watched the blank screen condition. For the experimental conditions, 10 individuals watched both scenarios; five individuals watched only the first, shorter scenario, one of whom watched only one outcome of the longer scenario. One individual only watched one outcome of the shorter scenario. There were three instances where individuals watched only one out of the three loops. Two of these instances were due to a technical error. In the third instance, a female (PE) struggled to stay for all three loops. In this case, she had watched loops 1 and 2 multiple times but would not stay for the third. We thus ended up showing her the outcome following only one loop. As she had seen the loop before on more than one occasion, we did not code her looking time to loops 1 and 2. There were three instances where chimpanzees watched only two out of the three loops. In one instance, a female (KL) missed the third loop but viewed the outcome. In the other two instances, we purposely played only two loops to one male (DA) as he did not have the attention span to sit for longer.

5.9.1 Inter-coder reliability.

Inter-coder reliability for looking time was significant for all conditions, however when examining differences between coders in looking time, both the blank screen condition, $r_s = .75$, $p = .04$; V = 0, $p = .02$, $n = 8$, and loop 2, $r_s = .75$, $p < .001$; V = 47.5, $p = .02$, $n = 25$, were significantly different between raters. Loop 1, $r_s = .90$, $p < .001$; V = 76.5, $p = .06$, $n = 26$, loop 3, $r_s = .73$, $p < .001$; V = 88.5, $p = .55$, $n = 24$, and the outcome condition, $r_s = .95$, $p < .001$; V = 46, $p = .05$, $n = 26$, all exhibited no significant difference in looking time between raters.

5.9.2 Blank screen vs. video.

Looking time to the video was significantly higher than looking time to the blank screen, $t(13) = -4.88$, $p < .001$. Mean proportion looking time to the blank screen was 0.14 ($SD = 0.09$), and mean proportion looking time to loop 1 was 0.39 ($SD = 0.22$). Thus chimpanzees appeared to engage with the screen significantly more when footage is playing than when footage is not playing.

5.9.3 Looking time to loops.

Looking time towards each scenario loop decreased on average across views. Proportion looking time loop 1, mean = 0.41, $SD = 0.28$, $n = 51$; proportion looking time loop 2, mean = 0.33, $SD = 0.31$, $n = 49$; proportion looking time loop 3, mean = 0.32, $SD = 0.27$, $n = 47$. This supports our first prediction that if participants engage with video content and recognise the scenario after first view, they should show habituation to the footage through decreased looking time in the second and third viewings.

5.9.4 Looking time to outcomes.

Mean proportion looking time for all outcomes was 0.43 (*SD* = 0.37, *n* = 52). As predicted, looking time to the outcome increased relative to looking time to the third loop, demonstrating that chimpanzees look longer at novel content. Examining differences in looking time to outcomes, we found a significant effect of outcome, with longer looking time towards the 'expected' outcome than the 'unexpected' outcome, *b* = -0.31, *SE* = 0.13, 95% CI = [-0.59, -0.07]. There was no significant difference in looking time between scenario type, *b* = -0.17, *SE* = 0.14, 95% CI = [-0.48, 0.11], or for the scenario x outcome interaction, *b* = 0.10, *SE* = 0.20, 95% CI = [-0.25, 0.51]. Participants looked longer at the emotional outcome scene, suggesting that they do not find the 'unexpected' outcome surprising.

5.9.5 Personality and looking time.

Chimpanzees who were higher in Neuroticism looked significantly longer at the outcomes. When we added age and sex to the model, the effect of Neuroticism was still significant (see Table 5.13). In the interaction model, the effect of Neuroticism remained significant. There was a steeper linear relationship between Neuroticism and looking time for the emotional outcome (Figure 5.3), but the interaction was not significant. Counter to our predictions, Openness was not associated with looking time to the scenario outcomes.

Table 5.13

Personality, age and sex (top) and Neuroticism x outcome interaction (bottom) as predictors of proportion looking time to scenario outcomes

	b	l-95%, u-95% CI	*SE*
	Looking time ~ personality		
Intercept	1.48	0.70, 2.30	0.44
Outcome	**-0.27**	**-0.45, -0.09**	0.10
Dom	0.47	0.00, 1.02	0.26
Ext	-0.19	-0.53, 0.18	0.18
Con	0.05	-0.29, 0.37	0.17
Agr	0.07	-0.28, 0.41	0.18
Neu	**0.54**	**0.04, 1.07**	0.26
Opn	0.08	-0.22, 0.40	0.16
Sex	-0.31	-0.86, 0.24	0.25
Age	-0.01	-0.04, 0.01	0.01
	Looking time ~ Neuroticism x outcome		
Intercept	1.00	0.78, 1.24	0.11
Outcome	**-0.30**	**-0.51, -0.13**	0.10
Neu	**0.29**	**0.07, 0.54**	0.12
Outcome x Neu	-0.21	-0.45, 0.00	0.11

Note. Dom = Dominance, Ext = Extraversion, Con = Conscientiousness, Agr = Agreeableness, Neu = Neuroticism, Opn = Openness. Significant effects highlighted in bold.

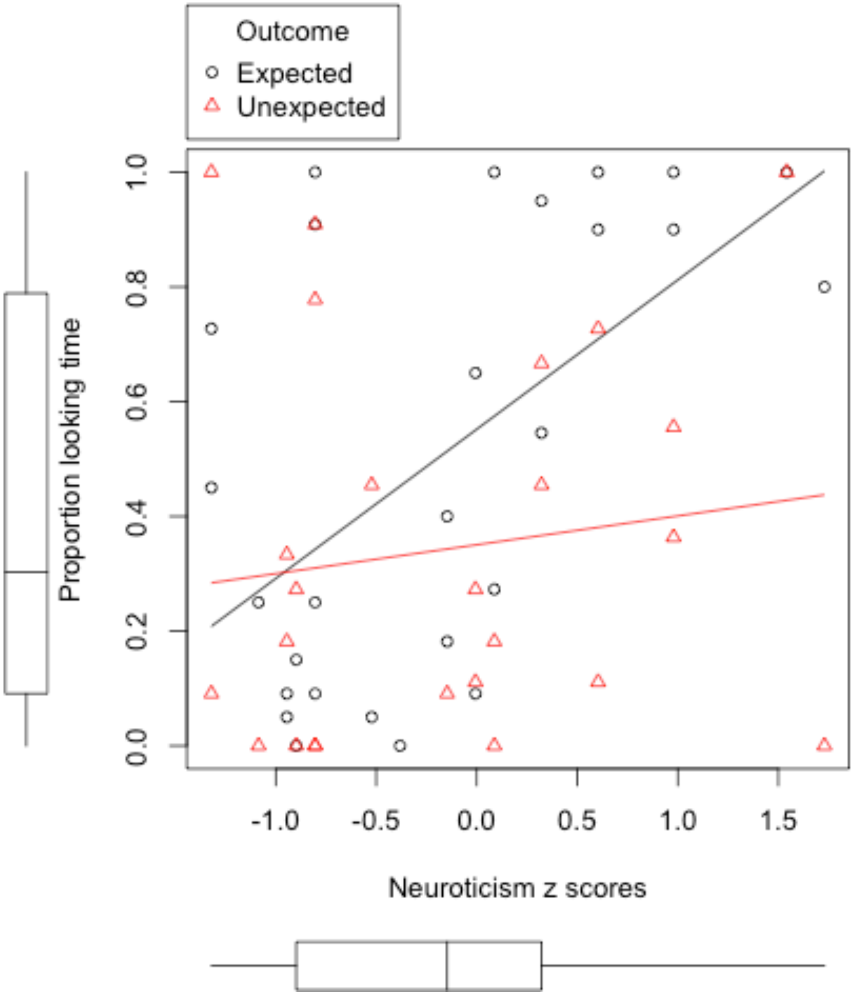


Figure 5.3

Association of Neuroticism with proportion looking time to the emotional and unemotional scenario outcomes.

5.10 Discussion

Findings from the video study indicate that chimpanzees engage with video of conspecifics, as previous research has found (Hopper et al., 2012; Morimura & Matsuzawa, 2001; von Rohr et al., 2015), and that repeated viewing of the same content reduces attention to the footage. This suggests that chimpanzees recognise and lose interest in familiar footage. However, due to mean differences in coders' observations of chimpanzee looking time for both the blank screen condition and for the second repetition of the scenario, we should be cautious in interpreting this data.

We found that chimpanzees looked significantly longer at the 'expected' emotional outcome, than at the 'unexpected' unemotional outcome. This suggests that they do not find the unexpected outcome surprising. Previous research has found that looking time can indicate violation of a social expectation. In addition to the use of videos to examine social expectations in chimpanzees (von Rohr et al., 2015), playback experiments in baboons showed that females looked longer towards the sound when they heard a call sequence that was inconsistent with their knowledge of social hierarchy (Cheney, Seyfarth, & Silk, 1995; Seyfarth et al., 2005). Thus, if chimpanzees had found the unexpected outcome surprising, they should have looked at it for longer. As we found that they directed more attention to footage of negative emotional valence, it seems likely that their response was based on interest in emotional valence, consistent with previous findings (Kano & Tomonaga, 2010; von Rohr et al., 2015), rather than expectation. However, the interpretation of looking time in this study is limited by the fact that, with only two outcome conditions, we cannot separate expectation from emotional valence. Thus we are unable to be conclusive in our understanding of why the chimpanzees looked longer at the emotional/expected outcome. For example, perhaps they looked longer at this condition because they experienced empathy for the subject.

Whilst these findings provide no evidence for emotional causality in chimpanzees, there are several other possible interpretations of the data to consider.

One possibility is that the chimpanzees failed to understand the scene continuity and thus were unable to interpret the outcome as a causal result of the prior conflict scenario. Another possibility is that they did grasp the scene continuity, but the outcomes were neither expected nor unexpected to them. Perhaps chimpanzees do not have social expectations about how conspecifics should respond when involved in conflict. As consolation and reconciliation play a strong role in post-conflict behaviour, a more relevant outcome might have been to show consolation or reconciliation responses following the conflict, rather than just differences in emotion. It is also possible that chimpanzees recognise that the footage is not real, a form of processing referred to as Equivalence (Fagot, Thompson, & Parron, 2010). The problem with this interpretation is that, even if they recognise that the footage is not real, this does not mean they will not form an emotional response or expectation to that footage, just as humans do when watching TV dramas or video clips (Kanske et al., 2015; Kim, 2012; Sood & Rogers, 2000). These findings call for further research that explores chimpanzees' ability to understand emotional causality from video footage.

Possibly the most novel finding of this study is that neurotic individuals look longer at the scenario outcomes. In the observational part of this study we found that Neuroticism was positively associated with Look behaviour towards all emotional events within the group. It is interesting to observe that the relationship between Neuroticism and looking behaviour translates across these two contexts. Although we were unable to establish whether chimpanzees display a causal knowledge of emotionality akin to cognitive empathy, the multilevel assessment of emotional perception allows us to address whether there are correlations between these different levels of emotional perception.

5.11 Part 3: Examining 'levels' of Perception

It has been suggested that humans have separate neural systems for emotional empathy and perspective taking (Shamay-Tsoory, 2011; Shamay-Tsoory et al., 2009). Recent evidence supports this, indicating mostly separate regions of neural activation for cognitive and affective empathy (Kanske et al., 2015; Moore et al., 2015). To some extent, chimpanzees show similar patterns to humans of responses to emotions. Although we do not know if chimpanzees have separate neural systems for different response types, evidence from this study suggests that they do have different response types, supporting the idea of different levels of emotional perception (de Waal, 2008; Trevarthen, 1979), and consistent with previous research that demonstrates emotional arousal and emotional recognition in chimpanzees (Parr, 2001; Parr & Hopkins, 2000). In Chapter 1, I grouped these responses into five levels. The purpose of this was so I could assess responses at different levels, and examine whether there was co-variation in these different response types.

In the behavioural part of this study, we examined individual differences in response to emotional events in others, and found that response type was predicted by personality. We first examined overall responsiveness as a measure of emotional awareness. In addition we examined behavioural responses, with the aim of assessing behaviours related to emotional contagion/arousal as well as emotional awareness.

We were able to examine four types of behavioural response, including Look, Move, Arousal and Interact. Interact was not related to personality, but the former three behaviours were. I proposed that Look behaviour is a measure of emotional awareness (level 2), and that emotional awareness seems to occur independently of either Arousal or Move. Arousal contains the items *sway* and *hoot*, which indicates that it is a measure of a level 1 response, that is, an automatic, contagious response, where an individual's emotional state may match the state of a conspecific (Hatfield et al., 1994). Where Move fits into these definitions of response types is less clear, although it may indicate curiosity in the event, suggesting that it could also fit as a measure of emotional awareness (level 2). We were unable to get enough data to examine sympathetic behaviours (level 3). We also did not attempt to measure emotional empathy (level 4), which is defined as emotional recognition accompanied by matching the emotional state of a conspecific. However, it is possible that behaviours such as Look and Move, which fit into emotional awareness, could also map onto emotional empathy if accompanied by a change in emotional state (de Waal, 2008).

Evidence in humans suggests that, to some extent, emotional empathy and perspective taking are correlated (Jolliffe & Farrington, 2006; Sulpizio et al., 2015). The former study found a significant relationship between the affective and cognitive scales of the Basic Empathy Scale (BES), with a mean of $r = .42$ across males and females (Jolliffe & Farrington, 2006). The latter study found that higher scores on emotional empathy were correlated with quicker performance on a spatial perspective taking task ($r = -0.30$). To understand the relationship of behavioural responses at different levels in chimpanzees, we decided to examine if there was an association between, firstly, Move and Look behaviours, and secondly, between Arousal and Look/Move behaviours. I predicted that (1) if Move is a measure of emotional awareness, it should be correlated with Look in response to events, and (2) if arousal responses and emotional awareness do represent different levels of processing, then Arousal will not be correlated with Look or Move.

This far, we have identified response types at two out of five levels of emotional perception. In the above experiment, we aimed to assess cognitive empathy (level 5). Although the results indicate that, at least under the method we used, chimpanzees do not demonstrate cognitive empathy, we observed individual differences in their attention towards the scenario outcomes. We found that some individuals looked longer than others, and chimpanzees with higher Neuroticism tended to look longer. Thus, we can examine whether there are associations in response types at different levels and whether there is any association between responses across group and experimental contexts. That is, does responsiveness in a group context predict responses in an experimental context? I predicted that (3) overall responsiveness in a group setting will be related to looking time to the experimental scenario outcomes, and (4) frequency of looking behaviour in a group setting will be related to looking time to the scenario outcomes.

5.12 Methods

5.12.1 Analyses.

To examine the relationship between behavioural frequencies in the group context, we ran three generalised linear mixed models. In the first two models, Look was the dependent variable, chimpanzee was a random effect and either Move or Arousal were fixed effects. In the third model, Arousal was the dependent variable, with Move as the fixed effect and chimpanzee as the random effect. We generated 95% confidence intervals using the Wald method.

To examine the relationship between looking time to scenario outcomes in the experiment and mean responsiveness to group emotional events, we ran a linear mixed model with proportion looking time to the scenario outcomes as the dependent variable. We calculated mean looking time for each chimpanzee for each outcome type, so each individual had a mean value for both the emotional and unemotional outcomes. Proportion looking time was arcsine transformed. We included chimpanzee as a random effect in the model, and fixed effects of scenario outcome type, responsiveness to group events and an outcome x responsiveness interaction.

Finally, we tested the relationship between looking behaviour within the social group and looking time to the video scenario outcomes. We calculated total instances of looking time to all events for each chimpanzee. We then split the data into mean looking time to the unemotional outcome and mean looking time to the emotional outcome. For each subset, we ran a linear model with arcsine transformed proportion looking time as the dependent variable and looking instances as the independent variable. We log transformed the looking instances as data were positively skewed. For the linear and linear mixed models we generated bootstrapped 95% confidence intervals for 500 samples.

5.13 Results

For our first prediction, we found that Look and Move were significantly, negatively associated, OR = 0.37, *SE* = 0.18, *p* < .001, 95% CIs [0.26, 0.52], supporting the suggestion that Move is a measure of emotional awareness. For our second prediction, there was no significant association between Arousal and Move, OR = 1.29, *SE* = 0.23, *p* = .26, 95% CI [0.83, 2.02] or between Arousal and Look, OR = 1.20, *SE* = 0.26, *p* = .48, 95% CI [0.72, 2.02], suggesting that Arousal occurs independently of behaviours associated with emotional awareness.

Thirdly, for proportion looking time to outcome, we found no significant effect of outcome, *b* = 0.71, *SE* = 0.75, 95% CI [-0.80, 2.18], responsiveness, *b* = 1.64, *SE* = 1.06, 95% CI [-5.01, 3.76], or outcome x responsiveness interaction, *b* = -1.55, *SE* = 1.19, 95% CI [-3.97, 0.77]. Counter to our prediction, awareness-based responses to emotional events do not generalise across contexts. Finally, we found no relationship between looking behaviour in the group and looking time, to either the emotional outcome, *b* = 0.19, *SE* = 0.2, *p* = .40, 95% CI [-0.28, 0.67] or the unemotional outcome, *b* = -0.003, *SE* = 0.25, *p* = .99, 95% CI [-0.54, 0.53].

5.14 Discussion

Our results suggest that Look and Move are both measures of emotional awareness, which occur independently of Arousal behaviour. This is consistent with the notion that chimpanzees experience different empathetic processes, which vary in both the behaviour they produce and the extent to which these processes are automatic or dependent on perspective taking (Berntson et al., 1989; de Waal, 2008; de Waal & Aureli, 1996). Notably, Arousal was comprised of behaviours *sway* and *hoot*, which, in conjunction with decrease in nasal temperature, have been observed in response to conflict footage (Kano et al., 2016). Kano's results support the idea that behaviours such as swaying and vocalising are primarily a reflexive, unconscious response to emotional stimuli. There is not enough evidence here to support the notion of a 'layering' system of emotional perception (de Waal, 2008), but that is not to say that it does not exist. Rather, the evidence presented here simply suggests that behavioural responses to emotions can occur at different levels. To understand to what extent these different processes are linked, or whether upper-level, perspective taking abilities are bound by lower-level, contagious responses, we would need to address responses more extensively, examining sympathetic and empathetic behaviours in relation to emotional contagion and emotional awareness. Whilst our study failed to get enough data points on sympathetic behaviour to analyse sympathetic responses, previous studies of post-conflict behaviour have observed behaviours such as consolation (de Waal & Aureli, 1996; Fraser et al., 2008; Romero et al., 2010). Thus, the study of empathetic behaviours may require a more focused approach of data collection than the one conducted in this study; for example, focusing only on dyadic conflicts and examining third party responses to conflict outcomes.

Whilst here I only identified two of the five levels of emotional perception that I outlined prior to this study, I believe these findings provide a good basis for further examination of the different ways that chimpanzees respond to emotions. In particular, it would be interesting to explore to what extent consolation behaviour in chimpanzees is dependent on emotional awareness or arousal, that is, is there some kind of emotional prerequisite for consolation to occur?

The last aim of this study was to examine whether responses to group situations correlated with responses to similar emotional stimuli viewed on video in an experimental setting. We found no association between responsiveness within the social group and looking time to the video footage. It is possible that responsiveness is not a meaningful measure unless accounting for event type. We also found no relationship between looking in response to events and proportion looking time to emotional and unemotional outcomes for the video footage. This suggests that response in a group context does not predict response to video stimuli, however possibly the lack of relationship is due to the differences in measures between each context. That is, in the experiment we focused on measuring looking time, whilst in the group contexts we focused on type of behavioural response – the two do not necessarily equate. Yet it is not unreasonable to expect that different measures of emotional perception should correlate. For example in humans, people that reported higher trait empathy showed increased neural activity in prefrontal brain regions associated with perspective taking, in response to scenarios demonstrating social exclusion (Masten, Morelli, & Eisenberger, 2011). Neural activity was also associated with prosocial behaviour towards the excluded victim. These findings suggest links between emotional empathy and perspective taking in humans. Further research in nonhuman primates should explore whether affective behaviours such as consolation relate to how individuals respond to emotional stimuli such as images or video footage.

5.15 Overall Discussion: Bringing Together the Findings

Observations from this study identified at least two levels of response behaviours under the umbrella term ‘emotional perception’. Consistent with our hypotheses, we also found that individuals vary in how they respond to emotional events in conspecifics. Whilst we found some effects of age and sex on response type, we also found evidence that personality is associated with both how much individuals respond, and how they respond. In particular, we found a number of associations between Neuroticism and response, as well as for Openness, Agreeableness and Dominance. We found only one significant association each for Conscientiousness and Extraversion with response. These results suggest that response to events of an agonistic nature, such as we studied here, are not simply dependent on an individual’s social ranking and may be determined by, for example, how easily aroused or attentive a chimpanzee is.

The associations between personality and response behaviours show some parallels to human personality traits associated with empathy. Chimpanzees higher on Agreeableness showed more frequent arousal responses to emotional events. In parallel, Friendliness has been associated with an index of human empathy (Barrio et al., 2004), and Agreeableness has been associated with affective empathy, empathic concern and cognitive empathy in humans (Jolliffe & Farrington, 2006; Mooradian et al., 2011). This suggests that the associations between personality and emotional perception may in part have emerged in a chimp-human ancestor. However we also found the opposite relationship for emotional awareness – lower Agreeableness was associated with a higher frequency of looking behaviour in chimpanzees. To understand the inter-specific similarities in the relationship of personality to different types of empathy would require a more direct comparison of personality/empathy measures between chimpanzees and humans.

We found that Neuroticism was negatively related to moving in response to conflict, but positively related to both look and arousal behaviour across all events. Neuroticism correlates with personal distress as well as empathetic concern in humans (Mooradian et al., 2011) and with affective empathy (Jolliffe & Farrington, 2006) although this latter finding was only significant in females. This suggests that Neuroticism may be an important factor to consider in measuring chimpanzees' affective responses to emotions, such as arousal and sympathetic concern.

In humans, Openness is associated with cognitive empathy (Jolliffe & Farrington, 2006) and with facets of fantasy, perspective taking and empathic concern (Mooradian et al., 2011). Although we found no association between Openness and response on the video task, we did find that Openness was associated with moving in response to conflict, which we believe is a measure of emotional awareness. Further research could benefit from a comparative understanding of emotional perception in chimpanzees and humans. For example, comparing attention or arousal between species in response to matching emotional stimuli.

Whilst the observational part of this study revealed some interesting relationships between personality and responses measuring emotional perception, there are some limitations to this study. Firstly, the behavioural definitions of the event categories were intentionally broad. By examining not only conflict and displays but also related behaviours, this allowed us to assess in which emotional contexts personality predicted response. The limitation in this approach is that our categories allowed for some overlap, meaning each event type was not entirely independent of the others. To address this, we propose that further research could focus specifically on one event type – such as conflict or displays only – to examine the relationship between personality and responses to events in more detail. To help understand to what extent emotional arousal and contagion are linked to other response types, it would be useful to record physiological responses in addition to behavioural responses. For example, measuring heart rate responses or changes in skin temperature (Berntson et al., 1989; Parr & Hopkins, 2000). This could be particularly useful to understanding individual differences in response, given that heart rate variability has been associated with personality (Briefer et al., 2015).

An additional variable that we did not address here was the identity of conspecifics involved in the events. The focus of this study was to assess how personality predicts response to conspecifics, rather than to assess how chimpanzees responded to a conspecific based on their relationship to that individual. However, given that similarities in personality traits have been implicated in friendships amongst chimpanzees (Massen & Koski, 2014), it would be worth assessing whether response to emotional events is determined by the strength of social bond amongst group mates involved.

In the experimental part of this study, we aimed to assess whether chimpanzees demonstrate cognitive empathy. The chimpanzees responded by looking longer at outcomes of negative emotional valence rather than outcomes that should violate expectations. There are several possible explanations for this finding. One possibility is that the chimpanzees did not grasp the continuity and causality of the scenario, and thus looked longer at the emotional outcome because it was more interesting. An alternative explanation is that they did understand the association between the scenario and the outcome: they looked longer at the outcome because they experienced emotional empathy - a matching of their emotional state to that of the chimpanzee on screen, combined with an awareness of that individual's emotion. Further assessment should thus examine whether chimpanzees are emotionally aroused when watching these scenes. One approach to this could be to measure changes in skin temperature through thermal imaging, which has been previously used to measure stress (Edgar, Nicol, Pugh, & Paul, 2013; Ludwig, Gargano, Luzi, Carenzi, & Verga, 2007; McGreevy, Warren-Smith, & Guisard, 2012), emotional state (Nakayama, Goto, Kuraoka, & Nakamure, 2005; Vianna & Carrive, 2005) and response to emotional stimuli (Kano et al., 2016; Kuraoka & Nakamura, 2011) in a number of species. Further studies could also assess whether altering the scenario results in changes to chimpanzees' looking time to the outcomes, thus assessing their causal knowledge of the scenario with the outcome.

The final part of this chapter examined whether responses at different levels, and in different contexts, are associated. We found no association between responsiveness assessed by behavioural observations and looking time to video footage in the experimental setting. Notably, overall responsiveness was unrelated to personality, whereas examining responsiveness at the level of each event type did reveal several relationships with personality. Thus it is possible that it is more meaningful to measure responsiveness at the level of each event, rather than taking an average measure per chimpanzee across all contexts. We also found no association between looking behaviour in the group and looking time to the outcomes. It is possible that this lack of relationship is due to the different ways that looking behaviour was measured in each context. Again, we did not account for context of the event in this analysis, which could also explain the lack of relationship; for example, a response measure that includes responses to submissive pant grunts is not necessarily going to reflect a response to conflict-related stimuli. Further examination of the relationship of responses across different contexts could help to shed more light on these findings.

Bringing these results together, the findings presented here consider chimpanzees' responses to primarily negative emotional stimuli: in the behavioural study, this included response to display, hoots, conflict and submissive interactions, and in the experimental study this included response to conflict. It is interesting to consider how these findings might have differed if we had used primarily positive emotional stimuli. Most likely, these would have been of less interest to the chimpanzees, given that previous findings indicate that negative emotional stimuli such as agonism and infanticide produce the longest looking times (Kano & Tomonaga, 2010; von Rohr et al., 2015). Given the frequency of aggression and displays in chimpanzee society, paying attention to agonistic behaviours seems important. However, perhaps there is also benefit to monitoring positive social relationships, such as who grooms with who or plays with who. Whilst I would predict that attention to these social events would be less so than attention to agonistic events, perhaps we are also likely to see different patterns of attention in relation to personality for these events, such as more extraverted individuals showing more frequent looking instances to positive emotional events.

To summarise, findings from this study indicate that personality plays a potentially important role in perception and response to emotions in conspecifics. Evidence also points towards arousal behaviours and awareness behaviours being separate levels of response that occur independently of one another. Tentatively, this could point towards the idea of separate neural systems of processing emotional events, as in humans (Kanske et al., 2015; Shamay-Tsoory, 2011; Shamay-Tsoory et al., 2009; Moore et al., 2015). Although measures of awareness do not measure perspective taking directly, they do rely on attention and so could be a prerequisite to cognitive empathy in chimpanzees. Whether chimpanzees have cognitive empathy in and of itself remains to be seen. We strongly encourage further research into the relationship between personality and emotional perception, particularly through addressing physiological changes that might underlie behaviour. Using individual differences to understand emotional perception could provide insight into the origins of empathy and its underlying mechanisms.

Chapter 6. Personality and Facial Morphology in Brown Capuchins

> *"The face provides a plethora of social information about an individual's gender, age, familiarity, emotional expression and potentially their intentions and mental state."*
>
> - Nathan J. Emery (2000, p. 582)

6.1 What's In a Face?

In chapters 4 and 5, I demonstrated that personality can be an important variable in how individuals respond to others, whether it be in grooming relationships or in responding to emotional events such as conflict. But what about how individuals perceive personality in conspecifics? That is, how does one individual's personality affect how others respond to them? Seyfarth, Silk and Cheney (2012) demonstrated that female baboons are more likely to approach female conspecifics who are friendly, and are less likely to approach conspecifics who are aggressive or who tend to spend time alone. Personality also influences friendships: in both capuchins and chimpanzees, dyads similar in traits related to sociability have better quality relationships than dyads who differ on these traits (Massen & Koski, 2014; Morton et al., 2015). This suggests that individuals preferentially associate with conspecifics who are similar in these traits, perhaps because it signals partner reliability (Massen & Koski, 2014). Thus, how an individual perceives certain traits in others is an important consideration when examining social interactions.

In humans, responses to the personality traits of other humans have been examined through work assessing links between facial dimensions and traits relating to aggression and dominance (Alrajih & Ward, 2013; Lefevre and Lewis, 2013; McCormick et al., 2008; Mileva et al., 2014). This work began with assessment of the facial width-to-height ratio (fWHR), a measure of bizygomatic face width divided by upper face height (Weston et al., 2004; see Figure 1, Wilson et al., 2014). Early work suggested that this was a sexually dimorphic trait, with men having wider faces than women (Weston, Friday, & Liò, 2007). More recent evidence suggests that the fWHR is not sexually dimorphic (Lefevre et al., 2012; Özener, 2012), and that observed differences between men and women can be accounted for by sex differences in body size (Kramer, 2015).

Despite this, an increasing number of studies are finding associations between fWHR and dominance-related traits in men, including aggression (Carré & McCormick, 2008; Carré, McCormick, & Mondloch, 2009), fighting ability (Trebicky et al., 2015; Zilioli et al., 2014), deception (Haselhuhn & Wong, 2011), untrustworthiness (Stirrat & Perret, 2010), cheating (Geniole, Keyes, Carré, & McCormick, 2014) and achievement striving (Lewis et al., 2012). fWHR has also been positively associated with perceptions of success, dominance and aggression in men (Alrajih & Ward, 2013; Lefevre & Lewis, 2013; Mileva et al., 2014).

Critics have argued that body weight mediates the association between fWHR and aggression (Deaner et al., 2012). However in further studies that controlled for body weight, fWHR remained a significant predictor of fighting performance (Trebicky et al., 2015; Zilioli et al., 2014), suggesting that the links between fWHR and dominance-related behaviour cannot be accounted for by simple differences in overall morphology. These associations may be linked to testosterone: one study found that wider male faces exhibit both higher baseline and reactive testosterone levels (Lefevre, Lewis, Perrett, & Penke, 2013), possibly mediating the relationship between fWHR and dominance-related behaviour through hormonal expression at both the behavioural and physiological level. However, more recent research indicates that fWHR does not increase with age as testosterone increases under adolescent development, and fWHR is only associated with testosterone after controlling for age (Hodges-Simeon, Sobraske, Samore, Gurven, & Gaulin, 2016). These results question the links between fWHR and testosterone, calling for further research on these associations.

Primate faces also communicate socially relevant information, such as emotional expression (Parr, Hopkins & de Waal, 1998; Visalberghi, Valenzano & Preuschoft, 2006), health (Stephen, Coetzee, Smith, & Perrett, 2009; Henderson, Holzleitner, Talamas, & Perrett, 2016) and fertility (Dubuc et al., 2009). Given the above-described findings in humans, we wanted to test whether similar associations can be found in nonhuman primates, and whether facial morphology is a cue to personality traits, by examining whether conspecifics respond to differences in facial morphology.

This would require recent personality ratings and access to facial images of sufficient quality. Such data were available for 64 brown capuchin monkeys (see Figure 6.1), *Sapajus apella* (see Alfaro, de Sousa Silva, & Rylands, 2012 for recent taxonomy change). Like humans, *S. apella* exhibit low sexual dimorphism in canine height, which according to Weston et al. (2004) is inversely related to sexual dimorphism in bizygomatic face width (although, this trend is disputed in humans, who exhibit low dimorphism in fWHR and canine height). Similarities with humans in canine height dimorphism make *Sapajus* a suitable candidate for comparison with humans.

Initially, we examined associations between Assertiveness, one of five brown capuchin personality dimensions, alpha status, and fWHR (Lefevre et al., 2014)[14] (see Appendix D). Personality was assessed using keeper ratings, which revealed the presence of five components (Morton, Lee, Buchanan-Smith, et al., 2013). One of these components was labelled Assertiveness as it was defined by high loading traits such as bullying, aggressive and dominant (Morton, Lee, Buchanan-Smith, et al., 2013). Alpha status was determined by assessing individual monkeys' wariness of other group members, how sought out these individuals were for mating, the number of offspring they produced, the frequency in which they engaged in allogrooming, and their ability to take food from humans and other monkeys.

---

[14] This study was the idea of T. Bates; I collected the facial data and was involved in the analysis and write up, as well numerous revisions of the manuscript for publication.

Figure 6.1

The faces of brown capuchins, *Sapajus apella*, are important in social communication. Left: an alpha male accompanied by a female directs threats towards his neighbours. The face of the alpha male (centre) is visibly broader than the face of a subadult male (right).

Facial measures were taken from photographs (see Figure 1, Wilson et al., 2014). A mean of 4.69 (*SD* = 2.44) photographs per individual, taken within one calendar year, were used to calculate average metrics per monkey. We found that face width was sexually dimorphic in adults (> 5 years old). Males had wider faces than females, however these differences were mediated by sexual dimorphism in body weight. We also found that fWHR was positively associated with Assertiveness and alpha status in adult capuchins independently of age, sex and body weight. These findings indicated that among males and females, more dominant individuals had wider faces (Lefevre et al., 2014). Further examination of the data by Carré (2014) suggested that this relationship may be driven by non-alpha individuals, similar to findings in humans (Goetz et al., 2013).

These results suggest that facial characteristics related to dominance are not specific to humans, and may exist in multiple primate taxa. However it is as yet unclear what underlies this relationship. One possibility is that fWHR is associated with bite strength (Lefevre et al., 2014). A more laterally positioned zygomatic arch could afford greater bite strength, a trait linked to high levels of combat, to dominance in combat, and to mating success, in several vertebrate species (Husak, Lappin, Fox, & Lemos-Espinal, 2006; Jones, Ruff, & Goswami 2013; Lappin & Husak, 2005). A second possibility is that a wider face is indicative of a stronger skull that is able to withstand injury in conflict (Lefevre et al., 2014). Both suggestions would implicate sexual selection through male-male competition as a driver of sexual dimorphism in face width. An alternative suggestion is that mate choice has driven the relationship between male face width and dominance-linked behaviour. Recent evidence suggests that, at least in humans, wider male faces are perceived as more attractive by women when considering short-term relationships (Valentine, Li, Penke, & Perrett, 2014). Of course, it is possible that more than one selection pressure has driven this relationship between morphology and behaviour, perhaps with initial physical advantages in combat later playing into facial cues to competitors or would-be mates. One should also note that neither of the above suggestions addresses the relationship found between fWHR and assertiveness in female capuchin monkeys, unless we assume similar selection pressures have acted on both males and females in this species.

To better understand these associations we explored whether other traits were also associated with facial morphology, and whether other facial dimensions were involved. In humans, facial morphology measures other than fWHR include lower face/face height and face width/lower face height, which have been included in composite measures of masculinity. Unlike fWHR these facial features are sexually dimorphic and inversely correlated (Lefevre et al., 2012; Penton-Voak et al., 2001;

Pound, Penton-Voak, & Surridge, 2009). We chose these measures as they had not been independently explored in relation to traits related to dominance. We thus examined these measures, including fWHR, in relation to all five components of capuchin monkey personality – Assertiveness, Openness, Neuroticism, Sociability and Attentiveness. This study[15] was published in *Personality and Individual Differences* and is included in published format on the next page.

The following content has been published as:

Wilson, V. Lefevre, C. E., Morton, F. B., Brosnan, S. F., Paukner, A. and Bates, T. C. (2014). Personality and facial morphology: Links to assertiveness and neuroticism in capuchins (*Sapajus* [*Cebus*] *apella*). *Personality and Individual Differences, 58,* 89 – 94.

---

[15] This study was the idea of T. Bates; I ran the majority of the analyses and wrote the paper together with T. Bates and suggestions from other co-authors.

Personality and Individual Differences 58 (2014) 89–94

Contents lists available at ScienceDirect

Personality and Individual Differences

journal homepage: www.elsevier.com/locate/paid

Personality and facial morphology: Links to assertiveness and neuroticism in capuchins (*Sapajus* [*Cebus*] *apella*)

V. Wilson [a,b,*], C.E. Lefevre [c], F.B. Morton [b,d], S.F. Brosnan [e], A. Paukner [f], T.C. Bates [a,g]

[a] *Department of Psychology, University of Edinburgh, UK*
[b] *Scottish Primate Research Group, UK*
[c] *Department of Psychology, University of York, UK*
[d] *Psychology, School of Natural Sciences, University of Stirling, UK*
[e] *Department of Psychology and Language Research Centre, Georgia State University, Atlanta, GA, USA*
[f] *Laboratory of Comparative Ethology, Eunice Kennedy Shriver National Institute of Child Health and Human Development, National Institutes of Health, Department of Health and Human Services, Poolesville, MD, USA*
[g] *Centre for Cognitive Ageing and Cognitive Epidemiology, University of Edinburgh, UK*

ARTICLE INFO

Article history:
Received 6 June 2013
Received in revised form 8 October 2013
Accepted 13 October 2013
Available online 9 November 2013

Keywords:
Capuchin
Personality
Face morphology
Sapajus
Assertiveness
Neuroticism
Attentiveness

ABSTRACT

Personality has important links to health, social status, and life history outcomes (e.g. longevity and reproductive success). Human facial morphology appears to signal aspects of one's personality to others, raising questions about the evolutionary origins of such associations (e.g. signals of mate quality). Studies in non-human primates may help to achieve this goal: for instance, facial width-to-height ratio (fWHR) in the male face has been associated with dominance not only in humans but also in capuchin monkeys. Here we test the association of personality (assertiveness, openness, attentiveness, neuroticism, and sociability) with fWHR, face width/lower-face height, and lower face/face height ratio in 64 capuchins (*Sapajus apella*). In a structural model of personality and facial metrics, fWHR was associated with assertiveness, while lower face/face height ratio was associated with neuroticism (*erratic* vs. *stable behaviour*) and attentiveness (*helpfulness* vs. *distractibility*). Facial morphology thus appears to associate with three personality domains, which may act as a signal of status in capuchins.

1. Introduction

Human personality is associated with differences in important behaviours, ranging from work (Ferguson, Heckman, & Corr, 2011) to well-being (Weiss, Bates, & Luciano, 2008). Research into the biological and evolutionary origins of personality may be of value in understanding these associations. One approach is the examination of links between individual differences in facial structure and behaviour (Plavcan, 2012; Plavcan, Vanschaik, & Kappeler, 1995; Weston, Friday, Johnstone, & Schrenk, 2004), including personality (e.g. Kramer & Ward, 2010; Penton-Voak, Pound, Little, & Perrett, 2006). For instance, facial width-to-height ratio (fWHR: the ratio of the bizygomatic-width to upper face height: see Fig. 1) shows links to dominance–like traits (Carré & McCormick, 2008) though not all studies have found these to be significant (Deaner et al., 2012; Özener, 2012). fWHR has also been associated with achievement striving (Lewis, Lefevre, & Bates, 2012), and with deception and untrustworthiness (Haselhuhn & Wong, 2012; Stirrat & Perrett, 2010).

Recently, links between personality and facial phenotype have been reported by Lefevre et al. (submitted for publication) in a non-human species, the brown capuchin monkey (*Sapajus apella*). Similar to humans, capuchin fWHR predicted individual differences in assertive behaviour and alpha status. Such findings therefore suggest that comparative studies between humans and non-human primates may shed light on the biological and evolutionary basis of appearance-personality associations.

Here we extend this initial work with the same population of capuchins. Because both personality and facial morphology are multi-dimensional, we assessed two additional measures of facial morphology, previously found to be sexually dimorphic in humans (Penton-Voak et al., 2001), but not previously assessed in non-human primates. Second, we moved beyond the single personality trait of assertiveness available to Lefevre et al. to include the full five domains of the Hominoid Personality Questionnaire (Weiss et al., 2009) assessed in capuchins (Morton et al., 2013).

The two new facial metrics assessed were lower face/face height, and face width/lower face height (see Fig. 1). Unlike fWHR (which shows species-specific differences in sexual dimorphism: Kramer, Jones, & Ward, 2012; Lefevre et al., 2012; Özener, 2012), both face width/lower face height and lower face/face height are

---

* Corresponding author at: Department of Psychology, University of Edinburgh, UK. Tel.: +44 131 651 1945.
E-mail addresses: v.a.d.wilson@sms.ed.ac.uk, tim.bates@ed.ac.uk (V. Wilson).

0191-8869/$ - see front matter © 2013 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.paid.2013.10.008

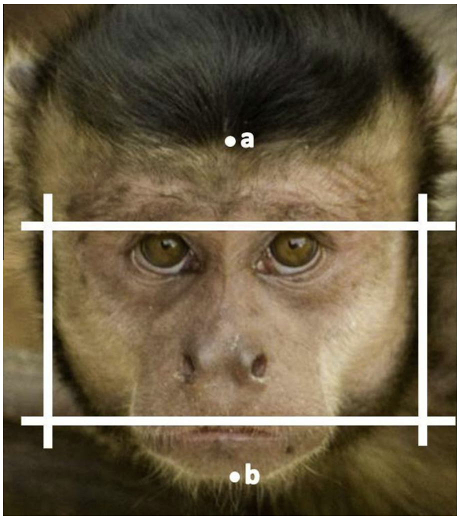


Fig. 1. Measures and measuring points used for morphometric calculations. *Note:* Horizontal lines show the distance between the upper lip and highest point of the eyelids (upper face height), vertical lines show the bizygomatic width. fWHR was calculated as width divided by height using these spans. Face width/lower face height was calculated as the bizygomatic width divided by the distance between the highest point of the eyelids and the lowest point of the chin (marked "b"). Lower face/face height was calculated as the distance between the highest point of the eyelids and the lowest point of the chin divided by the length of the whole face (a–b).

reliably sexually dimorphic in humans (Lefevre et al., 2012; Penton-Voak et al., 2001). Human face width/lower face height is correlated with fWHR, whereas lower face/face height may be independent of fWHR (Lefevre et al., 2012), and the two are weakly inversely correlated (Penton-Voak et al. (2001). We used a broad assessment of personality – the Hominoid Personality Questionnaire (Weiss et al., 2009), assessing five personality domains in capuchins: Assertiveness (identified by item loadings on *Bullying/Aggressive* vs. *Gentle/Cautious*); Openness (*Inventive/Inquisitive* vs. *Quitting*); Attentiveness (*helpfulness* vs. *distractibility*); Neuroticism (*erratic* vs. *stable behaviour*), and Sociability (*Affectionate, Friendly* vs. *Solitary/Depressed*) (Morton et al., 2013).

Given the evidence for an association between fWHR and assertiveness, and the relative independence of assertiveness from other dimensions of personality (Morton et al., 2013), we predicted that assertiveness would remain as the key indicator of fWHR, even after controlling for other personality variables. Secondly, we wished to establish whether the two additional facial metrics discussed above are sexually dimorphic in capuchins. Penton-Voak et al. (2001) reported that lower face/face height was inversely correlated ($r = -0.32$) with face width/lower face height in humans. We therefore tested the association of the two new facial metrics to personality, and whether these were independent predictors or shared variance of personality traits. To our knowledge, neither has been tested for association with personality in either humans or non-human primates. We tentatively predicted that, like fWHR, face width/lower face height would be associated with assertiveness in capuchins based on its shared dependence on face width. The possible links of lower face/face height to personality are unclear, and thus were not specified ahead of analysis.

2. Method

2.1. Sample

The sample consisted of 64 individuals of *Sapajus* recruited across three sites. 6 females (mean age 8.2 ± 4.0 years) and 10 males (mean age 11.4 ± 13.4 years) were recruited from the Living Links to Human Evolution Research Centre, University of St Andrews, Edinburgh Zoo (Macdonald & Whiten, 2011). The Language Research Center, Georgia State University provided 13 females (mean age 15.3 ± 11.8 years) and 9 males (mean age 10.9 ± 5.8 years). Finally 10 females (mean age 12.8 ± 9.2 years) and 16 males (mean age 6.6 ± 4.5 years) were recruited from the Laboratory of Comparative Ethology at the National Institute of Health. The study was non-invasive, approved by local ethics committees, and complied with the 2012 regulations of the Association for the Study of Animal Behaviour.

2.2. Facial measures

Measures were based on frontal facial photographs. Prior to measurement, photographs were horizontally aligned and scaled according to inter-pupillary distance (using the Psychomorph software package; http://users.aber.ac.uk/bpt/jpsychomorph (Tiddeman, Perrett, & Burt, 2001). fWHR was then computed as the ratio of bizygomatic-width (maximum horizontal distance from the left to the right facial boundary) to upper face height (vertical distance from the mid-point of the upper lip to the highest point of the eyelids; see Fig. 1). Lower face/face height and face width/lower face height (Penton-Voak et al., 2001) were calculated as shown in Fig. 1. Measurement reliability was good (ICC = .86) based on a subset of photographs ($N = 18$) measured twice. In addition, measures from several photographs per individual (mean = 4.69, SD = 2.44) were averaged in order to maximise the signal to noise ratio. All images were taken within 1 calendar year, thus controlling for longitudinal changes.

2.3. Personality measures

The personality ratings were collected for each animal individually using the Hominoid Personality Questionnaire (Weiss et al., 2009). This 54-item measure has been validated in chimpanzees (*Pan troglodytes*) (Weiss et al., 2009), orang-utans (*Pongo spp.*) (Weiss, King, & Perkins, 2006), rhesus macaques (*Macaca mulatta*) (Weiss, Adams, Widdig, & Gerald, 2011), and brown capuchin monkeys (Morton et al., 2013). The items consist of adjective markers, accompanied by one to three short behavioural descriptions. For example, the item *Fearful* is described as "*Subject reacts excessively to real or imagined threats by displaying behaviors such as screaming, grimacing, running away or other signs of anxiety or distress.*" Items are scored on a 7-point Likert scale ranging from 1: display either total absence or negligible amounts of the trait, to 7: display extremely large amounts of the traits.

All personality data used in this study are described fully in Morton et al. (2013). Briefly, ratings were collected for 127 monkeys. Between one and seven raters, each familiar with the monkeys, conducted the ratings, and to maintain independence of scoring were asked not to discuss their ratings with other raters. Inter-rater reliability was calculated for all monkeys with two or

Table 1
Means (and standard deviations) for personality dimensions and facial metrics.

Trait	Female	Male
Assertiveness	3.79 (1.13)	3.88 (0.93)
Openness	4.03 (0.69)	4.40 (0.69)
Sociability	4.74 (0.67)	4.74 (0.72)
Attentiveness	4.68 (0.65)	4.79 (0.54)
Neuroticism	4.0 (0.61)	4.10 (0.53)
fWHR	2.14 (0.14)	2.20 (0.17)
Face width/lower face height	1.41 (0.08)	1.45 (0.09)
Lower face/face height	0.75 (0.04)	0.74 (0.04)

Table 2
Table of zero-order correlations among all personality and face variables. $N = 64$ for all cells.

	Attentiveness	Neuroticism	Assertiveness	Openness	Sociability	Lower face/face height	fWHR	Face width/lower face height
Attentiveness	1.00	−0.53	0.02	0.14	0.54	−0.31	0.14	0.17
Neuroticism	−0.53	1.00	0.00	0.34	−0.40	0.18	−0.19	−0.25
Assertiveness	0.02	0.00	1.00	0.08	0.22	−0.04	0.52	0.27
Openness	0.14	0.34	0.08	1.00	0.34	−0.35	−0.03	−0.19
Sociability	0.54	−0.40	0.22	0.34	1.00	−0.22	0.22	0.07
Lower face/face height	−0.31	0.18	−0.04	−0.35	−0.22	1.00	0.02	−0.11
fWHR	0.14	−0.19	0.52	−0.03	0.22	0.02	1.00	0.45
Face width/lower face height	0.17	−0.25	0.27	−0.19	0.07	−0.11	0.45	1.00

more raters ($n = 121$). Reliability of items are reported in Morton et al. (2013). For the whole sample, the number of components to extract was determined using parallel analysis. Five components – assertiveness, openness, attentiveness, neuroticism, and sociability – were extracted using Principal Components Analysis (see component descriptions above). Personality scores for the current sample were based on this analysis; all but 3 monkeys in our sample were rated by two or more raters. Each factor was validated against observations of behaviour within monkey's social groups, and to how individuals responded to cognitive testing (Morton et al., 2013; Morton, Lee, & Buchanan-smith, 2013). Inter-rater reliabilities and behavioural validation support personality ratings as valid measures of primate personality, and refute arguments of anthropomorphism (Weiss et al., 2009).

3. Results

Descriptive statistics for the measured variables, and correlations among the personality dimensions and facial metrics, are shown in Tables 1 and 2 respectively. We found a strong association between the two width-based measures (fWHR and face width/lower face height; $r = .45$, $p < .001$), suggesting they share variance and may both be linked to assertiveness. Lower face/face height was independent of both fWHR ($r = .02$, $p = .90$) and face width/lower face height ($r = -0.11$, $p = .11$).

We first examined associations of fWHR to personality traits besides assertiveness. A regression model was constructed with fWHR as the dependent variable and entering all five personality traits – openness, neuroticism, attentiveness, assertiveness and sociability – as independent variables with covariates of age, age^2, sex, age × sex (See Table 3). This model was significant ($F(9,54) = 6.66$, $p < .001$, adjusted $R^2 = 0.45$) and replicated the previously reported significant age × sex interaction ($F(1,54) = 14.36$, $p < .001$) and the association of fWHR with assertiveness ($F(1,54) = 12.71$, $p < .001$). However, no other personality dimensions approached significance for association with fWHR (see Table 3).

We next examined associations between the two new facial metrics and personality using identical regression models to those used for fWHR above (See Table 3). For face width/lower face height (full model: $F(9,54) = 3.15$, $p < .001$, adjusted $R^2 = 0.23$) a significant age × sex interaction was found ($F(1, 54) = 5.87$, $p = .02$), with sex differences increasing across the life span (see Fig. 2). These findings of significant sex differences in face width/lower face height are compatible with data from humans, in which face width/lower face height is also dimorphic (Penton-Voak et al., 2001). To explicitly test the sexual dimorphism of this trait, models not including personality were also run. Face width/lower face height showed both a main effect of sex ($F(1,59) = 4.09$, $p = 0.047$), and a significant age × sex interaction ($F(1,59) = 8.39$, $p = 0.005$), with males and females showing higher and lower ratios with age, respectively (Fig. 2).

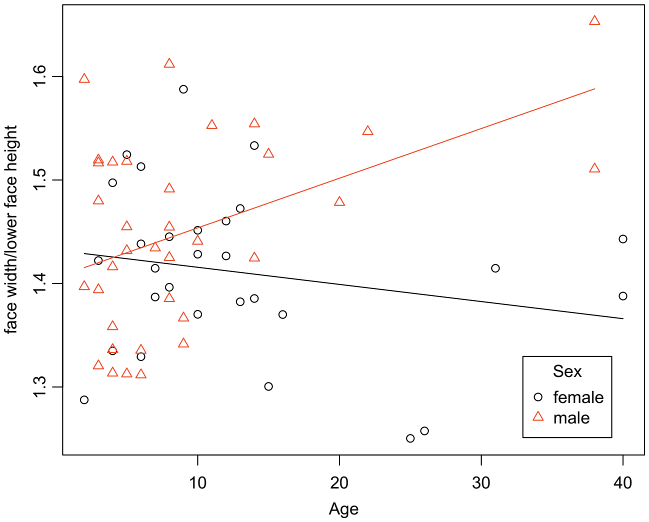


Fig. 2. Linear fits of age against face width/lower face height, separately for each sex.

Assertiveness (but no other personality dimension) showed a significant association with face width/lower face height ($F(1,54) = 6.47$, $p = .014$). This association, however, did not appear to account for additional unique variance in assertiveness over and

Table 3
Regression of fWHR and face width/lower face height on demographic variables and personality (n = 64).

	fWHR				face width/lower face height			
	Est.	SE	*t*	*P*-value	Est	SE	*t*	*P*-value
Age	0.004	0.008	0.557	0.579	−0.013	0.005	−2.493	0.016
Sex	−0.069	0.049	−1.405	0.166	−0.021	0.033	−0.638	0.526
Age^2	−0.000	0.000	−1.796	0.078	0.000	0.000	2.002	0.050
Assertiveness	0.058	0.016	3.566	<0.001	0.028	0.011	2.543	0.014
Openness	−0.008	0.032	−0.244	0.808	−0.039	0.022	−1.822	0.074
Neuroticism	−0.053	0.041	−1.297	0.200	−0.038	0.027	−1.404	0.166
Sociability	0.018	0.032	0.576	0.567	−0.018	0.021	−0.866	0.390
Attentiveness	−0.039	0.039	−1.098	0.277	0.006	0.024	0.267	0.791
Age × Sex	0.013	0.004	3.789	<0.001	0.006	0.002	2.422	0.019

above fWHR: adding fWHR to the model rendered the association of face width/lower face height with assertiveness non-significant ($F(1, 53) = 2.12$, $p = .151$). This finding suggests that face width/lower face height taps the same underlying biological variance that relates fWHR to assertiveness in capuchins.

Turning to lower face/face height, we again examined associations with personality using regression models with lower face/face height as the dependent variable, covariates of age, age^2, and sex and independent predictors of assertiveness, openness, attentiveness, neuroticism and sociability as conducted above for the width-based metrics (full model: $F(9, 54) = 2.85$, $p = .008$, adjusted $R^2 = 0.21$). There was a significant effect of age ($F(1, 54) = 6.01$, $p = .017$), but no significant evidence for sexual dimorphism (i.e., no effects of sex or age × sex interaction: see Table 3). This lack of dimorphism was confirmed in a simpler model containing just age, with age^2 and age × sex as predictors: Lower face/face height increased with age ($F(1,59) = 4.33$, p = 0.04) but showed no sex or age × sex effects ($p = 0.63$ and 0.75 respectively). In humans, both neuroticism (Costa & McCrae, 1992) and lower face/face height are dimorphic (Penton-Voak et al., 2001). We thus tested for dimorphism in neuroticism in the present sample of capuchins, but found it to be non-dimorphic ($F(1, 62) = 0.56$, $p = 0.45$).

Examining associations of lower face/face height with personality, associations were found with both neuroticism and attentiveness. Higher neuroticism was associated with greater lower face/face height ratios ($F(1, 54) = 6.25$, $p = .015$, see Fig. 3). However, depending on the order of entry into the model, both attentiveness and neuroticism showed links to lower face/face height. Because of this potential association with two simultaneous personality outcomes, we utilised structural equation modelling (SEM) to produce an integrated model of fWHR and lower face/face height with assertiveness, neuroticism and attentiveness.

SEM allows a test of the hypothesis that the association of lower face/face height is best modelled, either as being specific to one or other of these traits (with the apparent association to both traits simply reflecting covariance among the traits in this sample); or, by contrast, that lower face/face height influences both neuroticism and attentiveness, thus accounting in part for their overlapping behavioural elements (see Fig. 4). Simultaneously we can examine the impact of fWHR, its links to lower face, and their joint impact on assertiveness. Our base model is shown in Fig. 4. This fit well ($X^2(6) = 7.11$, RMSEA = 0.054, CFI = 0.981, TLI = 0.968), indicating that the width and height based facial measures are well accounted for as separate (uncorrelated) influences on the three personality traits. Dropping the path from lower face/face height to either attentiveness or to neuroticism reduced model fit significantly ($\chi^2(1) = 14.39$, $p = .0001$ and $\chi^2(1) = 6.59$, $p = .0034$, respectively). Lower face/face height, then, appears, to directly influence both attentiveness and neuroticism.

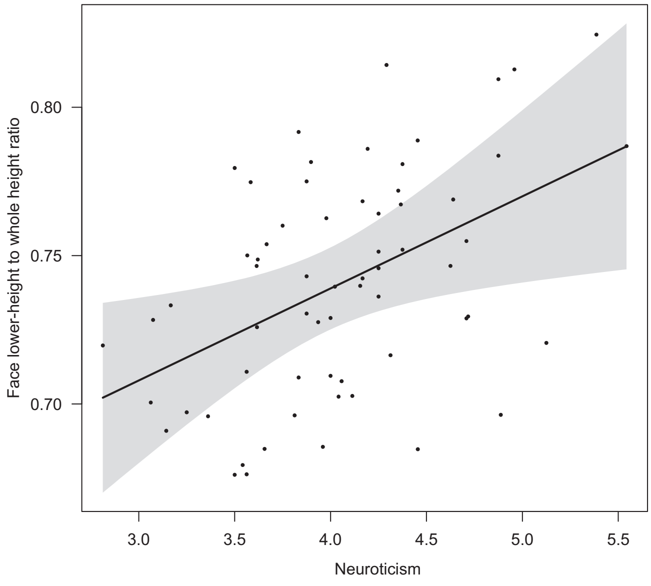


Fig. 3. Regression plot of lower face/face height against Neuroticism.

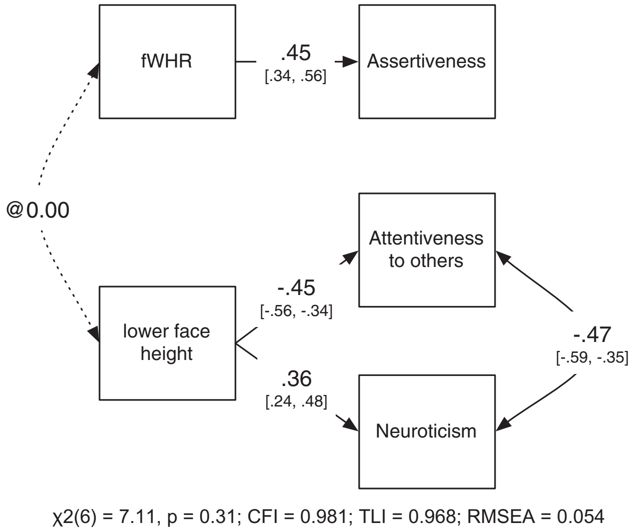


Fig. 4. Structural equation model predicting Assertiveness, Attentiveness to others, and Neuroticism from fWHR and lower face/face height. Note: Standardized path coefficients shown [95% confidence intervals in brackets]. Model fit was good according to CFI, TLI, and RMSEA.

4. Discussion

We tested the association of three facial metrics with five personality dimensions in 64 capuchins (*Sapajus apella*). fWHR and face width/lower face height associated with assertiveness even after controlling for the other four personality dimensions, with fWHR accounting for this association. In contrast, a higher ratio of lower face/face height (i.e., relatively longer lower face) was significantly associated with higher neuroticism and lower attentiveness scores. The results suggest that facial morphology reliably reflects three major personality domains: assertiveness, attentiveness and neuroticism, via two uncorrelated morphological ratio measures.

The present study extends the previously reported association of relative facial width to assertiveness (Lefevre et al., submitted for publication) by examining the full spectrum of personality and an additional width-linked facial feature: face width/lower face height. To our knowledge, the association of face width/lower face height with assertiveness per se has not been evaluated in any primate species (including humans). Unlike human fWHR (Kramer et al., 2012; Lefevre et al., 2012; Özener, 2012), face width/lower face height is sexually dimorphic in humans (Penton-Voak et al., 2001) with women showing higher ratios than men. In the present sample we also found dimorphism of face width/lower face height, however males showed higher ratios than females, a difference that increased with age. The association with assertiveness shown here, then, suggests that it would be informative to assess the relationship of face width/lower face height to behaviour in large human samples of both sexes, perhaps controlling for neuroticism, which was linked to face height.

The question of why these three facial metrics relate to assertiveness, attentiveness, and neuroticism is open. Given the paucity of literature on this issue, we speculate that a common factor is a link to status and leadership traits (Lilienfeld et al., 2012). Work in humans has suggested that status is best conceived of as two orthogonal dimensions based, respectively, on coercion and pro-social competence (Henrich & Gil-White, 2001). The association of face-width metrics with a more aggression-linked capacity for dominance clearly fits with links of fWHR to testosterone (Lefevre, Lewis, Perrett, & Penke, 2013; Penton-Voak & Chen, 2004), and thus fits the coercion profile. Consistent with the interpretation that traits associated with lower face/face height share links to pro-social competence, the two traits linked to lower face/face height (neuroticism and attentiveness) are both associated with vigilance and with attention span in cognitive testing. The association with lower face/face height, then, may be driven primarily by the markers these two traits share, namely vigilance and attention span (Morton et al., 2013). Such attentive behaviour appears to confer status not by aggression, but via a "policing" role associated with reduced time in play and increased time in vigilant attention (Flack, Girvan, de Waal, & Krakauer, 2006). Thus lower face/face height may be linked to this second, social, form of status. Such pro-social monitoring status, shown here to relate to lower face/face height ratio, may presage the prestige-earning dimension of status found in humans (Henrich & Gil-White, 2001).

In seeking human personality dimensions compatible with "policing", the most likely candidate would appear to be the HEXACO Honesty-humility dimension which is based on duty, caution, and being self-effacing (Ashton & Lee, 2007). It would be valuable to test links of lower face/face height ratio in humans to Honesty-humility and to ratings of admiration in others. A similar dimension – 'Equable' – has been reported in rhesus macaques, which, like attentiveness, is associated with reduced play (Weinstein, Capitanio, & Gosling, 2008). It would thus be useful to examine face morphological links in rhesus macaques.

Openness and sociability were unrelated to any of the facial metrics. In capuchins, openness is related to task participation and learning performance, while sociability is related to social contact and alert behaviour (Morton et al., 2013; Morton, Lee, & Buchanan-Smith, 2013). The present findings suggest that, at least in capuchins, openness and sociability play a role in sociality and cognition, but independently of status drive or achievement. In addition, and in distinction to human research, we did not find sexual dimorphism for neuroticism or for lower face/face height ratios in capuchins. Both these traits are dimorphic in humans (Del Giudice, Booth, & Irwing, 2012; Penton-Voak et al., 2001). Sexual dimorphism for personality may, then, be linked to dimorphism in morphology, with these dimorphisms varying across species under distinct social and sexual selection pressures. Addressing species differences in social structure, cognition and behaviour may help to establish what determines species-specific personality traits, and why they are associated with facial morphology.

In summary, these results shed light on biomarkers of personality, and on personality differences across species. It would benefit to have sufficient power to explore in more detail the significant sex-specific age growth in capuchin facial metrics, as well as to examine effects of location and body weight in relation to these findings. Additional studies examining the lower face/face height metric in other species would be valuable, and may shed light on the origins of status effects on well-being and emotional traits linked to status in humans (Wood, Boyce, Moore, & Brown, 2012).

Acknowledgements

We thank everyone involved in the personality study, especially Alexander Weiss, Phyllis Lee, Bernard Thierry, and Hannah Buchanan-Smith. We also thank Mark Bowler, Andrew Whiten and Nicolas Claidiere, for providing photos and permissions for collecting photos at Living Links, and Catherine Talbot for providing photos of the Language Research Center capuchins. Finally we thank Alexander Weiss and Gary Lewis for their advice with data analysis.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.paid.2013.10.008.

References

Ashton, M. C., & Lee, K. (2007). Empirical, theoretical, and practical advantages of the HEXACO model of personality structure. *Personality and Social Psychology Review, 11*(2), 150–166 [doi: 10.1177/1088868306294907].

Carré, J. M., & McCormick, C. M. (2008). In your face: Facial metrics predict aggressive behaviour in the laboratory and in varsity and professional hockey players. *Proceedings Biological Sciences/The Royal Society, 275*(1651), 2651–2656 [doi:10.1098/rspb.2008.0873.

Costa, P. T., Jr., & McCrae, R. R. (1992). *Revised NEO personality inventory-professional manual*. Florida: Psychological Assessment Resources Inc.

Deaner, R. O., Geary, D. C., Puts, D. A., Ham, S. A., Kruger, J., Fles, E., et al. (2012). A sex difference in the predisposition for physical competition: Males play sports much more than females even in the contemporary US. *PLoS One, 7*(11), e49168 [doi: 10.1371/journal.pone.0049168].

Del Giudice, M., Booth, T., & Irwing, P. (2012). The distance between Mars and Venus: Measuring global sex differences in personality. *PLoS One, 7*(1), e29265. http://dx.doi.org/10.1371/journal.pone.0029265.

Ferguson, E., Heckman, J. J., & Corr, P. (2011). Personality and economics: Overview and proposed framework. *Personality and Individual Differences, 51*(3), 201–209 [doi: 10.1016/J.Paid. 2011.03.030].

Flack, J. C., Girvan, M., de Waal, F. B., & Krakauer, D. C. (2006). Policing stabilizes construction of social niches in primates. *Nature, 439*(7075), 426–429. http://dx.doi.org/10.1038/nature04326.

Haselhuhn, M. P., & Wong, E. M. (2012). Bad to the bone: facial structure predicts unethical behaviour. *Proceedings Biological Sciences/The Royal Society, 279*(1728), 571–576 [doi:10.1098/rspb.2011.1193].

Henrich, J., & Gil-White, F. J. (2001). The evolution of prestige: Freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evolution and Human Behavior, 22*(3), 165–196 [doi: S1090513800000714].

Kramer, R. S., Jones, A. L., & Ward, R. (2012). A lack of sexual dimorphism in width-to-height ratio in white European faces using 2D photographs, 3D scans, and anthropometry. *PLoS One, 7*(8), e42705. http://dx.doi.org/10.1371/journal.pone.0042705.

Kramer, R. S., & Ward, R. (2010). Internal facial features are signals of personality and health. *Quarterly Journal of Experimental Psychology, 63*(11), 2273–2287. http://dx.doi.org/10.1080/17470211003770912.

Lefevre, C. E., Lewis, G. J., Bates, T. C., Dzhelyova, M., Coetzee, V., Deary, I. J., et al. (2012). No evidence for sexual dimorphism of facial width-to-height ratio in four large adult samples. *Evolution and Human Behavior, 33*(6), 623–627. http://dx.doi.org/10.1016/J.Evolhumbehav. 2012.03.002.

Lefevre, C. E., Lewis, G. J., Perrett, D. I., & Penke, L. (2013). Telling facial metrics: Facial width is associated with testosterone levels in men. *Evolution and Human Behavior, 34*(4), 273–279. http://dx.doi.org/10.1016/J.Evolhumbehav. 2013.03.005.

Lefevre, C. E., Wilson, V. A. D., Morton, F. B., Brosnan, S. F., Paukner, A., & Bates, T. C. (submitted for publication). Facial width-to-height ratio predicts dominance in capuchin monkeys. PLoS One.

Lewis, G. J., Lefevre, C. E., & Bates, T. C. (2012). Facial width-to-height ratio predicts achievement drive in US presidents. *Personality and Individual Differences, 52*(7), 855–857. http://dx.doi.org/10.1016/j.paid.2011.12.030.

Lilienfeld, S. O., Waldman, I. D., Landfield, K., Watts, A. L., Rubenzer, S., & Faschingbauer, T. R. (2012). Fearless dominance and the US presidency: Implications of psychopathic personality traits for successful and unsuccessful political leadership. *Journal of Personality and Social Psychology, 103*(3), 489–505. http://dx.doi.org/10.1037/a0029392.

Macdonald, C., & Whiten, A. (2011). The living links to human evolution research centre in edinburgh zoo: A new endeavour in collaboration. *International Zoo Yearbook, 45*, 7–17.

Morton, F. B., Lee, P. C., & Buchanan-Smith, H. M. (2013). Taking personality selection bias seriously in animal cognition research: A case study in capuchin monkeys (*Sapajus apella*). *Animal Cognition, 16*(4), 677–684. http://dx.doi.org/10.1007/s10071-013-0603-5.

Morton, F. B., Lee, P. C., Buchanan-Smith, H. M., Brosnan, S., Thierry, B., Paukner, A., et al. (2013). Personality structure in brown capuchin monkeys (Sapajus apella): Comparisons with chimpanzees (Pan troglodytes), orangutans (*Pongo* spp.), and rhesus macaques (Macaca mulatta). *Journal of Comparative Psychology, 127*(3), 282–298. http://dx.doi.org/10.1037/a0031723.

Özener, B. (2012). Facial width-to-height ratio in a Turkish population is not sexually dimorphic and is unrelated to aggressive behavior. *Evolution and Human Behavior, 33*(3), 169–173. http://dx.doi.org/10.1016/j.evolhumbehav.2011.08.001.

Penton-Voak, I. S., & Chen, J. Y. (2004). High salivary testosterone is linked to masculine male facial appearance in humans. *Evolution and Human Behavior, 25*(4), 229–241.

Penton-Voak, I. S., Jones, B. C., Little, A. C., Baker, S., Tiddeman, B., Burt, D. M., et al. (2001). Symmetry, sexual dimorphism in facial proportions and male facial attractiveness. *Proceedings of the Royal Society B-Biological Sciences, 268*(1476), 1617–1623 [doi:10.1098/rspb.2001.1703].

Penton-Voak, I. S., Pound, N., Little, A. C., & Perrett, D. I. (2006). Personality judgments from natural and composite facial images: More evidence for a kernel of truth in social perception. *Social Cognition, 24*(5), 607–640.

Plavcan, J. M. (2012). Sexual size dimorphism, canine dimorphism, and male–male competition in primates where do humans fit in? *Human Nature, 23*(1), 45–67. http://dx.doi.org/10.1007/S12110-012-9130-3.

Plavcan, J. M., Vanschaik, C. P., & Kappeler, P. M. (1995). Competition, coalitions and canine size in primates. *Journal of Human Evolution, 28*(3), 245–276 [doi: 10.1006/Jhev.1995.1019].

Stirrat, M., & Perrett, D. I. (2010). Valid facial cues to cooperation and trust: Male facial width and trustworthiness. *Psychological Science, 21*(3), 349–354. http://dx.doi.org/10.1177/0956797610362647.

Tiddeman, B. P., Perrett, D. I., & Burt, D. M. (2001). Prototyping and transforming facial textures for perception research. *IEEE Computer Graphics and Applications, 21*, 42–50.

Weinstein, T. R., Capitanio, J. P., & Gosling, S. D. (2008). Personality in animals. In O. P. John, R. W. Robins, & L. A. Pervin (Eds.), *Handbook of personality* (3rd ed., pp. 328–348). NY: Guilford.

Weiss, A., Adams, M. J., Widdig, A., & Gerald, M. S. (2011). Rhesus macaques (*Macaca mulatta*) as living fossils of hominoid personality and subjective well-being. [Research Support, N.I.H., Extramural]. *Journal of Comparative Psychology, 125*(1), 72–83. http://dx.doi.org/10.1037/a0021187.

Weiss, A., Bates, T. C., & Luciano, M. (2008). Happiness is a personal(ity) thing: The genetics of personality and well-being in a representative sample. *Psychological Science, 19*(3), 205–210. http://dx.doi.org/10.1111/j.1467-9280.2008.02068.x.

Weiss, A., Inoue-Murayama, M., Hong, K. W., Inoue, E., Udono, T., Ochiai, T., et al. (2009). Assessing chimpanzee personality and subjective well-being in Japan. *American Journal of Primatology, 71*(4), 283–292. http://dx.doi.org/10.1002/ajp.20649.

Weiss, A., King, J. E., & Perkins, L. (2006). Personality and subjective well-being in orangutans (Pongo pygmaeus and Pongo abelii). *Journal of Personality and Social Psychology, 90*(3), 501–511. http://dx.doi.org/10.1037/0022-3514.90.3.501.

Weston, E. M., Friday, A. E., Johnstone, R. A., & Schrenk, F. (2004). Wide faces or large canines? The attractive versus the aggressive primate. [Comparative Study Research Support, Non-U.S. Gov't]. Proceedings Biological Sciences/The Royal Society, 271 Suppl 6, S416–419. doi: 10.1098/rsbl.2004.0203.

Wood, A. M., Boyce, C. J., Moore, S. C., & Brown, G. D. A. (2012). An evolutionary based social rank explanation of why low income predicts mental distress: A 17 year cohort study of 30,000 people. *Journal of Affective Disorders, 136*, 882–888.

6.2 Personality Measures in the Face

Previous research indicates the importance of the face in primate communication, through individual recognition (e.g. Parr & Hopkins, 2000; Pokorny & de Waal, 2009a; Pokorny & de Waal, 2009b) and communicating social information. Up to eight facial expressions have been observed in capuchins, which are similar across species (De Marco, Petit, & Visalberghi, 2008; Visalberghi, Valenzano & Preuschoft, 2006), and can communicate emotions in behavioural contexts, such as play, submission and affiliation. Similar expressions exist in other primates, such as chimpanzees, who exhibit a context-related understanding of emotion (Parr, Hopkins & de Waal, 1998; Parr, 2001; Parr & Waller, 2006).

The face also serves to communicate information useful for reproduction. In rhesus macaques (*Macaca mulatta*), facial skin colour signals female fertility (Dubuc et al., 2009), and in males, is believed to be a sexually selected trait, with females showing more social solicitations to males with dark red faces (Dubuc, Allen, Maestripieri, & Higham, 2014). Given the low levels of direct male-male competition in this species, Dubuc et al. (2014) suggest that skin colour is an ornament that evolved in response to female mate choice. Skin colouration may also be linked to status. In male mandrills (*Mandrillus sphinx*), drills (*Mandrillus leucophaeus*) and geladas (*Theropithecus gelada*), skin colouration has been associated with dominance and social status (Bergman, Ho, & Beehner, 2009; Marty, Higham, Gadsby, & Ross, 2009; Setchell, Smith, Wickings, & Knapp, 2008). Furthermore in humans, enhanced oxygenated blood colouration of the face is associated with perceptions of health, which may be used to assess mate quality and fitness in conspecifics (Henderson et al., 2016; Stephen et al., 2009).

All of the above findings suggest that both in nonhuman primates and humans the face is key to communicating social information, through emotional expression or colouration. It thus follows that facial morphology could also play a role in social interactions. Given that similarities in facial cues exist between humans and nonhuman primates, it is perhaps unsurprising that an association of fWHR with Assertiveness was found in a species of nonhuman primate. In two studies we examined associations of three measures of facial morphology and five dimensions of personality in brown capuchins. We found an association between face width and higher Assertiveness (Lefevre et al., 2014) and an association between lower face height and higher Neuroticism/lower Attentiveness (Wilson et al., 2014). These findings raise three questions. Firstly, do similar associations between facial morphology and personality exist in other species? Secondly, to what extent is the sexual dimorphism of facial morphology determined by species differences in social structure, intra-sexual competition and mate preference? Thirdly, do facial features signal certain traits, or is the relationship between morphology and personality simply due to physical advantages provided in combat?

Whilst it would be interesting to address all three questions, first, we should focus on better understanding the role of fWHR in capuchin social interactions. The next step is therefore to consider whether it is possible to test capuchins' response to traits in conspecifics through the use of facial images, and to establish a methodology that allows us to test their response to the faces of conspecifics.

Chapter 7. Is the Capuchin Face a Cue to Personality?

> *"The belief that faces portray character is ubiquitous. This persistence of lay theories of physiognomy is hard to credit…Nonetheless…. accurate perception of personality is possible from facial characteristics alone."*
>
> - Penton-Voak, Pound, Little & Perret (2006, p. 608)

7.1 Personality in the Face: Signals or Cues?

In chapter 6, I describe a relationship between fWHR and Assertiveness, as well as a relationship between face height and Neuroticism. Findings in humans have previously indicated that dominance-related traits can be perceived from the face (Alrajih & Ward, 2013; Lefevre & Lewis, 2013; Mileva et al., 2014). Such perceptions are not just limited to traits relating to the fWHR. Four out of five of the personality dimensions found in humans can also be determined from facial features, the exception being Conscientiousness (Kramer & Ward, 2010), although accuracy of perceptions varies with both the trait rated and whether individual or composite images are presented (Penton-Voak, Pound, Little, & Perrett, 2006).

Early attempts to link facial features to personality characteristics, known as physiognomy, were dismissed in the 20th century as pseudoscience (Graham, 1961; Penton-Voak et al., 2006). However, given the last century of progress dedicated to assessing personality, and further, the development of empirical measures which allow us to measure individual perceptions of others, our current understanding of face ratings are that they accurately reflect trait perceptions in others. These results appear less surprising when we consider that personality is associated with online behavioural patterns such as Facebook user activity (Bachrach, Kosinksi, Graepel, Kohli, & Stillwell, 2012) and can be perceived from both physical and online environments (Gosling, Ko, Mannarelli, & Morris, 2002; Vazire & Gosling, 2004). In humans, it seems relatively easy to assess traits in others given the multitude of cues at our disposal – a person's dress, interests, tidiness, time keeping and demeanour towards others all provide us with quick cues to their personality.

In nonhuman primates, such cues are not so easily available. However, our findings reported in Chapter 6 suggest that primate faces might be a cue to certain personality traits. This is not the first time it has been suggested that personality traits can be perceived in the faces of nonhuman primates. Kramer and colleagues (Kramer, King, & Ward, 2011; Kramer & Ward, 2012) found that traits relating to dominance can be perceived by untrained human observers in facial images of chimpanzees. It is possible that facial cues to dominance in chimpanzees are similar to those found in humans, making it possible for people to detect these traits easily (although, other traits are less easy to detect, such as sociable; see Kramer et al., 2011). It thus remains to be seen whether differences in facial morphology act as species-specific cues to certain traits amongst species of nonhuman primate.

We wanted to examine whether capuchins might be able to detect differences in such traits just by examining faces of different dimensions. By this, we are implying that the face is a cue or a signal to certain traits. Given the contention that differences in definition of these two terms have caused in the past, it is important to be clear on what we mean by the words 'cue' and 'signal'. Maynard Smith and

Harper (2003) provide clarification of the definitions of these terms: a cue is a feature that provides information to a receiver, but is not necessarily intended for the receiver, that is, it did not evolve because of its effect on the receiver. In contrast, a signal is a feature that provides information of interest to the receiver, and which evolved because of the effect it has on the receiver.

In chapter 6, I discussed the possibility that a wider face provides a physical advantage in combat. If this is the case, we cannot refer to differences in face size as a signal to others, unless a wider face evolved as a 'badge of status' (Dawkins & Krebs, 1978; Krebs & Dawkins, 1984), that is, to signal dominance and to resolve dispute without conflict. This would be particularly useful when interacting with conspecifics in the absence of social knowledge (i.e. with strangers) (Bergman & Sheehan, 2013).

Alternatively, differences in face size could have evolved through mate choice. It has been suggested that people mate assortatively for similar personality traits (Little, Burt, & Perrett, 2006). This is not entirely surprising given that, in nonhuman primates, individuals with similar traits tend to have better quality relationships (Massen & Koski, 2014; Morton et al., 2015). For example, in brown capuchins, dyad similarity in sociability is related to better relationship quality (Morton et al., 2015); similarly, in chimpanzees, frequency of contact sitting within a dyad is associated with similarities in sociability per dyad (Massen & Koski, 2014). However, intersexual selection is often driven by female preference for male traits. Given that in capuchins, personality-morphology correlates in the face are evident in both sexes, it is unlikely that this relationship is driven by mate choice alone. It is however possible that, given the sexually dimorphic nature of fWHR in capuchins (but notably, not of face height), consistent with the dual utility hypothesis (Berglund, Bisazza, & Pilastro, 1996), differences in face width first evolved through intrasexual competition, and later became a signal of fitness under mate preference.

As we have not yet measured how capuchins respond to face width in conspecifics, it is preferable for now to refer to fWHR as a potential cue. Although we previously found links between two facial measures and different personality traits, we decided to focus on testing perceptions of fWHR in capuchins, given that perceptions of fWHR have already been tested in humans. In the rest of this chapter I outline a study that attempted to assess this, and discuss the difficulties of this methodology.

7.2 Designing a Method to Test Response to Facial Morphology

This of course presents a number of methodological issues. Firstly, such tests cannot be run using familiar conspecifics as stimuli, because a subject's prior knowledge of that animal's dominance rank would bias the subject's response. The use of unfamiliar conspecifics could also cause ethical issues – introducing an unfamiliar animal to a new group can be stressful for all involved. Collecting data from chance introductions would be ethically grounded, but would result in too little data over too long a time frame to be worthwhile. For these reasons, the best option appeared to be to use facial images as experimental stimuli.

Previous experiments have relied on photographic stimuli for assessing social responses to particular facial features. For example, examining preference for facial symmetry (Waitt & Little, 2006), recognition of group members, or identification of facial expressions (Parr & Hopkins, 2000; Parr, 2001; Pokorny & de Waal, 2009a; 2009b). However, the use of still or moving images can also be problematic, as response is dependent on how the animal interprets an image. Fagot et al. (2010)

propose that there are three ways in which photos can be processed: Independence, Confusion and Equivalence. When a subject views an image, they may either not associate it with a conspecific (Independence), or alternatively, understand that the image is a representation of a conspecific, and thus not treat it as the real individual (Equivalence) (for example, this is how humans perceive a photograph). In either of these cases, the elicited response is not necessarily a reliable predictor of behaviour towards the same, real conspecific in the wild. Thus the animal has to perceive the image as real (Confusion) to give a response that is ecologically valid (Morton et al., 2016), meaning that care must be taken to assess the methodology prior to testing any social stimulus in captive primates.

With these issues in mind, we initially set out to examine whether response to photographs would provide a 'realistic' way of assessing response to live animals. To do so, we showed images of familiar conspecifics to captive capuchin monkeys from two locations (Living Links, Edinburgh Zoo and Language Research Centre (LRC), Georgia State University) (see Morton et al., 2016 for details; Appendix D)[1]. Photos depicted alpha individuals in the group (for definition of alpha, see Chapter 6) and responses to these images were compared with response to the conspecific depicted. There were four photo conditions: a full body image with direct gaze (n = 11); a 'floating' face with direct gaze (n = 11); a full body image with averted gaze (n = 18); and a 'floating' face with averted gaze (n = 18) (see Figure 7.1). Studies often make use of head only images (i.e. a 'floating face') (e.g. Griffey, 2011; Pokorny & de Waal, 2009a), however such images could be perceived as unrealistic, as animals rarely see a head that is detached from a body. Thus, we aimed to control for this by including full-body and head-only images. Eye gaze is an important part of facial

---

[1] This study was the idea of B. Morton. I contributed to conceptual and methodological discussions, collection of facial images for the experiment, general project coordination and manuscript edits.

communication, for example, direct gaze can be perceived as threatening in some species (Emery, 2000; van Hooff, 1962; van Hooff, 1967), hence it was important to control for gaze direction.

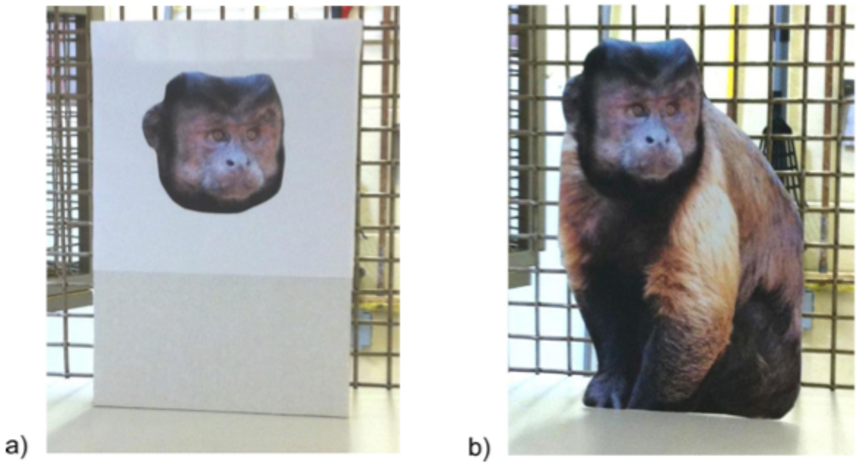


Figure 7.1

Images used for averted gaze conditions. (a) Image of a floating face and (b) image of a full body condition. *Recreated from Morton et al., 2016, with kind permission from Elsevier (Figure 1, © the Authors).*

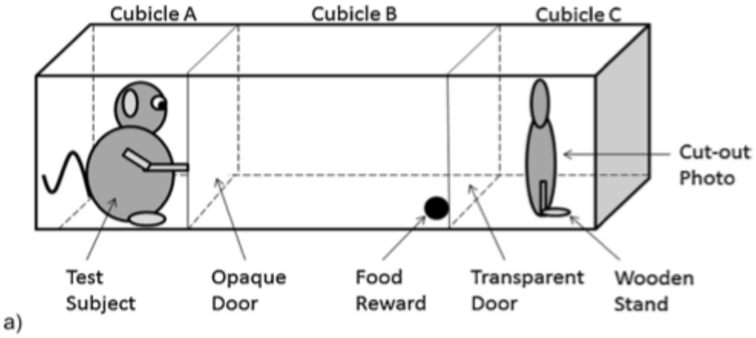


Figure 7.2

Experimental set up at Living Links. *Recreated from Morton et al., 2016, with kind permission from Elsevier (Figure 2, © the Authors).*

Response was measured using latency to approach either the photo or monkey within the research enclosure (for set up, see Figure 7.2). Lower ranking individuals tend to avoid being in close proximity to higher ranking group members (Fragaszy, Visalberghi, & Fedigan, 2004; Janson, 1990; Morton et al., 2014). Proximity data thus provides us with a reliable measure of how capuchins respond to each other in their daily environment. We predicted that subjects' latency to approach an alpha individual within the research enclosure would be negatively correlated with time spent in close proximity (within one body length) to that individual out with research hours. We further predicted that, if capuchins responded to the photos as if they were real, their response to the photo conditions would correlate with their response to the real monkeys within the research rooms.

Results revealed that response to the real monkey condition was significantly negatively correlated with time spent in close proximity to the real monkey (r = -.65). This suggests that monkeys' responses to conspecifics within the research cubicles reflect their associations with the same conspecifics in the enclosure at large.

However, latency to approach the photo conditions was not significantly associated with their latency to approach the real monkey condition (highest r = .57 (full body, averted gaze condition), or to time spent in close proximity to that monkey (highest r = -.46, full body, averted gaze condition). These findings suggest that capuchins do not respond to images of their counterparts as they would respond to the presence of the live monkey pictured in the image. Yet, the capuchins did differ in their responses between stimuli.

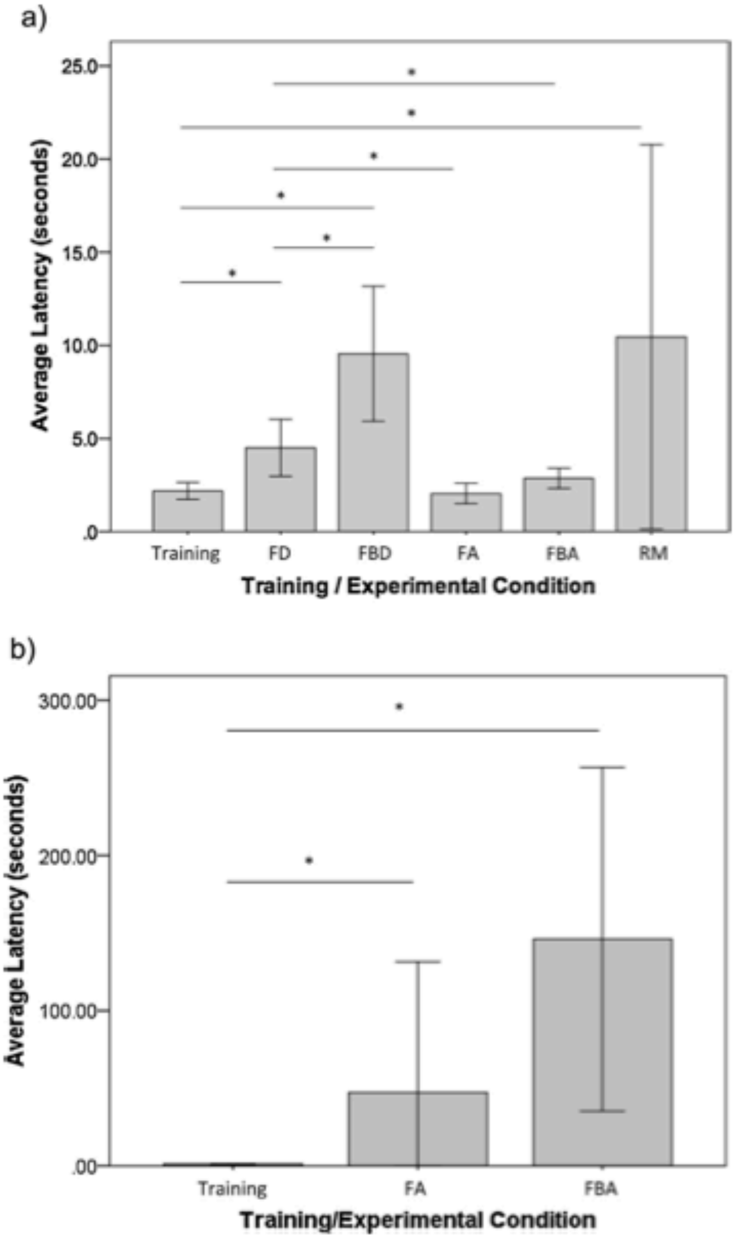


Figure 7.3

Average response latencies to each condition in each sample for (a) Living Links and (b) LRC. Training = approach in absence of social stimulus; FD=floating face, direct gaze; FBD = full body, direct gaze; FA = floating face, averted gaze; FBA = full body, averted gaze; RM = real monkey. *Recreated from Morton et al., 2016, with kind permission from Elsevier (Figure 3, © the Authors).*

On comparison of the differences in latencies between conditions, we found that latency to approach the full body image with direct gaze (mean difference in latency from baseline = -7.36) was significantly higher than the face only image with direct gaze (mean difference in latency from baseline = -2.32), and was not significantly different from mean latency to approach the real monkey condition (t = -0.17) (see Figure 7.3).

Overall, these findings indicate that the monkeys differentiate between the information presented by each image, and similarity in latency scores between the real monkey and full body direct gaze conditions suggests that they most likely perceived the full body direct gaze condition as the most 'life-like'. There are alternative explanations to their responses, for example, the full body images could simply have taken longer to process, resulting in delayed approach. Counter to this however, it is notable that their approach to the full body condition differed with whether the gaze was direct or averted. This, together with earlier studies measuring response to eye gaze in photographic stimuli (see Matsuzawa (2006) and Myowa-Yamakoshi (2006) for a discussion of these findings), suggests that their response is dependent on the social information provided by the image. Thus, although they do not react to the image as if it were real, they do process the social information in a realistic manner.

It is also possible that because the photo represented an image of a familiar conspecific, it provided confusing information, that is, it looked the same but did not smell or act the same. Although the use of images will always lack the behavioural and olfactory elements of a real conspecific, it is possible that such contrasts are less salient when the image is of a novel individual, particularly if important social information can be immediately extracted from the image. Thus, despite the limitations of the above study, we decided to use facial images to test capuchins' responses to variations in fWHR. In an attempt to use more ‘life-like’ stimuli that would potentially elicit a more realistic response from the monkeys, we decided upon a method that would incorporate 3D models with facial images. In using this method, our aims were two-fold: firstly, to examine whether monkeys differed in their responses to models of differing face width. Secondly, to control for the ‘novelty’ aspect of the models, we aimed to test whether monkeys differed in their response to real dominant vs. subordinate monkeys within the research cubicles. Thus, testing whether differences in response to the wide vs. narrow faced models reflect differences in response to dominant vs. subordinate conspecifics.

Using latency to approach as our measure of response, we predicted that 1) participants would be slower to approach unfamiliar models than familiar monkeys, 2) as capuchins tend to avoid close proximity to higher ranking group members (Janson, 1990) participants would be slower to approach the dominant than the subordinate monkey, and 3) if they perceived dominance from the unfamiliar faces, they would be slower to approach the wide faced model over the narrow faced model.

7.3 Methods

7.3.1 Sample.

We collected data from brown capuchin monkeys housed at the Living Links Centre, Edinburgh Zoo (MacDonald & Whiten, 2011). Monkeys were housed in two groups with symmetrical enclosures. The groups, totalling 35 monkeys (including six infants) lived in a mixed species environment with common squirrel monkeys (*Saimiri sciureus*), a design intended to replicate naturalistic conditions and provide enrichment (Leonardi, Buchanan-Smith, Dufour, MacDonald, & Whiten, 2010). Both groups had access to an indoor and outdoor enclosure, an off-show area and a research room (see Dufour, Sueur, Whiten, & Buchanan-Smith, 2011 for details).

The research rooms provided access from the monkeys' indoor and outdoor enclosure via a tunnel, to which the monkeys had access out with research hours. The tunnel consisted of two levels of four connected cubicles [each cubicle: H 52.1 cm x W 51.4 cm x L 49.5 cm] which could be closed off from each other via the use of a sliding door. This way monkeys could be separated from the group for research participation. Research slots took place twice a day on Mondays, Tuesdays, Thursdays and Fridays, from 11:15 to 12:45 and 14:15 to 15:45. Monkeys were trained to come into the research cubicles for food rewards, but all research participation was voluntary.

Data collection including training took place between 16 May 2014 and 7 July 2014. I collected all data, with the help of M. Gartner. We trained 21 monkeys to participate in our study. Of the 16 that passed training, 15 took part in testing. We removed data for one juvenile who participated in only the first experimental condition, but failed to approach the model, at which point that test session was aborted. Thus for our analyses we retained data for 14 monkeys, thirteen of which had completed testing. This sample consisted of 6 females and 8 males, between 3 and 19 years old (mean age = 7.57, *SD* = 4.78).

7.3.2 Model design.

Building on the use of photographic stimuli in our previous study, we decided that the use of full-body stimuli were the most realistic. We used facial photographs of real capuchins so we could manipulate fWHR, which was then attached to a 3D 'model' for the body.

Face.

Twelve images from 12 different male capuchins were manipulated for fWHR. Due to the effects of direct eye gaze revealed in the previous study, images with averted eye gaze were selected, and some images were mirror flipped to get them looking in the same direction. Following Stirrat and Perret (2010), the six highest and six lowest fWHR images were selected to form two composite images. For each group, average location of feature points were calculated. Images were transformed using the difference between the high fWHR and low fWHR group. Features for the high fWHR were adjusted by +50% of the difference between group averages, and features for the low fWHR were adjusted by -50% (see Figure 7.4). Image manipulations were courtesy of A. Little.

The two composite facial images were printed on canvas and each moulded to a separate ‘head’ made from papier mâché to give them a 3D appearance. We estimated head size based on measurements of the capuchins taken in the research cubicles, and by checking average head dimensions reported in the literature.

Body.

The body was made from papier mâché, and covered with a canvas print photograph of a capuchin body to retain a realistic appearance (see Figure 7.4). To control for body size, which is correlated with fWHR (Lefevre et al., 2014), we made one body which could attach to both heads interchangeably. We estimated the ‘body’ size based on the height of capuchins within the research cubicles, and by checking average body length measures reported in the literature. Developing model representations of peripheral body structures such as the limbs and tail was deemed unnecessary in our design, as to give the stimuli a more naturalistic feel, it would be placed behind a screen of foliage. In the wild capuchins often occupy dense foliage, meaning that parts of the body are often partially concealed from view (see Figure 7.5 for examples). We thus used a screen of foliage to conceal missing features and overall body size (see Figure 7.4). The purpose of the body was therefore to support the head, and to prevent the appearance of a 'floating face' effect.

Using a wooden stand inserted through the centre and out the top of the body, we could attach and detach each head, which also had wooden attachments at the back allowing them to be screwed in place.

Figure 7.4

Stages of model design. Top: composite unmasked images for low fWHR (left) and high fWHR (right). Middle: 3D model design with attached faces. Bottom: Model with narrow face (left) and wide face (right) concealed behind foliage screen within the research cubicles. This is the first view that the monkeys had of the models.

Figure 7.5

In the wild, capuchins often occupy dense foliage, meaning that parts of the body can be partially concealed from view. Photo credits: (left) dany13/flickr (CC), (middle) Rosenthal/flickr (CC), (right) Seligman/flickr (CC).

Foliage screen.

A transparent Perspex slide, made to fit the dimensions of the research cubicles, was painted with leaves using non-toxic green paint.

7.3.3 Procedure.

Following Morton et al. (2016) we used latency to approach the models as our measure of response.

Training.

To develop a baseline measure of latency to approach, and to accustom the monkeys to the foliage screen, we first trained participants to approach the screen to collect a high value food reward (piece of date) (see Figure 7.6).

A food reward was placed at the bottom of the foliage screen. At the start of each session, participants were held separately in a starting cubicle where they were given raisins as a reward for coming in to participate. This also gave them time to acclimatise to the set up. An opaque slide separated them from the cubicle containing the food reward (see Figure 7.6 for set up). When this slide was drawn back, participants would approach the foliage screen and collect the food reward. Using a stopwatch we timed how long it took each monkey to cross the cubicle, starting the timer as the door opened. Based on previous research we estimated that it should take them no more than three seconds to approach and collect the food reward. For each monkey, we continued the training sessions until they could complete this task within three seconds. Each participant was required to do this three consecutive times to show consistency before they could complete their training.

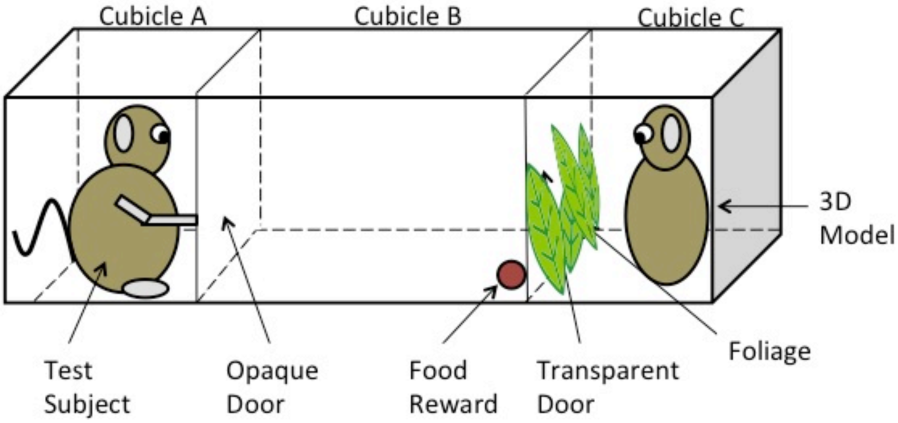


Figure 7.6

Experimental set up. Subject is housed in cubicle A. The opaque door prevents them from seeing the model, which is placed behind the foliage slide in cubicle C. When ready, the door to cubicle A is opened and the participant has to cross cubicle B and collect the food reward from the base of the slide.

Testing.

There were four experimental conditions:

1. Wide faced model (WFM)
2. Narrow faced model (NFM)

3. Dominant real monkey, i.e. alpha (DRM)
4. Subordinate real monkey (SRM)

In addition to having the two model conditions, we used real monkeys from each group to form the ‘real monkey’ condition. Alpha individuals were chosen for the dominant real monkey. In each capuchin group, there is only one alpha male and one alpha female (Janson et al., 2012). Subordinate monkeys were sub-adult males aged five years who did not have central positions in the social group. Their social positions were established through keeper observation, as well as through knowledge of developmental behaviour in maturing male capuchins. In the wild, as males approach maturity they become peripheral to their group, such as through receiving fewer grooming bouts (Di Bitetti, 1997) and emigrate from their natal group (Janson et al., 2012). As photos were of male monkeys, we used males for both real monkey conditions, with the exception of the male alpha in one group who would not be tested; in this case, we used the alpha female instead.

During testing, either the real monkey or the body of the model was concealed behind the foliage screen. Each participant saw all conditions, viewing each condition once. Viewing order was counterbalanced for whether individuals viewed the model or monkey first, whether they saw the dominant or subordinate first and whether they viewed the narrow or wide faced model first. Overall viewing order was randomised. No participant saw more than one condition in a day. After viewing each condition a ‘re-train’ session was required, to reduce the expectation of stimuli in subsequent conditions. In the re-train condition participants saw only the foliage slide, and as in the training condition were required to approach and get the food reward within three seconds, three consecutive times. If they did not succeed to do this after five attempts, we released them and repeated the re-train in the next available session.

Measures.

Latency to approach was recorded during the session using a stopwatch. To ensure accuracy of timings, all sessions were video recorded and latency was also coded from the videos.

7.3.4 Analyses.

All analyses were conducted in R version 3.0.2 (R Core Team, 2013).

Inter-rater reliability.

All videos (including baseline, experimental and re-train sessions) were coded by myself. To reduce the potential for coder bias, a second coder who was blind to the hypotheses also coded 50% of the videos (*n* = 193) which were selected at random. We ran three comparisons of interrater reliability using Spearman's rank correlations due to skew: 1) between stopwatch and my own video coded latencies, 2) between video codings of two independent coders (myself and one other) and 3) between stopwatch and video codings of the second coder.

Latency to approach.

We examined the effect of condition on latency to approach either the model or the real monkey. We used stopwatch timings for latency as they were accurate to the millisecond. Where stopwatch recordings were uncertain, we used video coding measures instead. We first tested, using a between subjects *t*-test whether latency to approach the alpha monkey differed between groups, given that we had one female and one male alpha.

We ran mixed effects models using the lmer function (Bates et al., 2015), with latency as the dependent variable, condition as the fixed effect and monkey ID as a random effect. As latencies were skewed, we transformed the data using a Yeo

Johnson power transformation for normalizing data (Weisberg, 2001). We also generated bootstrapped 95% confidence intervals for 500 samples.

First, we compared latency in all four conditions to baseline. As a baseline measure we took each individual's latency score for their last training session, prior to viewing all conditions. To check whether response was mediated by age or sex, we included these two variables as fixed effects in the first model. To examine our hypotheses regarding differences in latency to approach 1) models vs. real monkeys, 2) dominant vs. subordinate monkeys and 3) wide vs. narrow faced models, we re-ran model 1 including orthogonal contrast coding for these three effects. Finally, we re-ran the contrast model in the adult sample only (n = 8; defined as > 5 years old; see Izawa (1980)) to ensure that responses to the conditions were not affected by maturity.

7.4 Results

7.4.1 Training.

On average, the monkeys required 7.19 training sessions before they passed the training (*SD* = 5.34).

7.4.2 Interrater reliability.

Interrater reliabilities were high for all three measures (> .80). Stopwatch and coder 1: $r_s = .89, p < .001$; coder 1 and coder 2: $r_s = .82, p < .001$; stopwatch and coder 2: $r_s = .81, p < .001$.

7.4.3 Latency to approach.

Response to the alpha monkey did not differ between groups, $t(29.34) = 1.47$, $p = .152$. Our first model revealed that of the four conditions, the DRM and both model conditions had significantly longer approach latencies compared to the baseline condition (see Table 7.1). Adding age and sex to the model had no effect, and reduced model fit [model 1 AIC = 197.87, model 2 AIC = 198.97]. Model 3, which examined contrasts between baseline/all experimental conditions, real monkey/model, WFM/NFM and DRM/SRM, found no significant difference between the real monkey/model or the WFM/NFM conditions (see Table 7.2 and Figure 7.7). Latency to approach the dominant real monkey was marginally, significantly longer than latency to approach the subordinate. Our fourth model examined these effects in adults only (*n* = 8). There were no significant effects (see Table 7.2 and Figure 7.7).

Table 7.1

Latency to approach models vs. monkey conditions and with additional predictors of age and sex

	b	l-95%, u-95% CI	*SE*	*p*
		Latency ~ Condition		
Intercept	5.75	5.24, 6.32	0.27	< .001
DRM	**0.98**	0.11, 1.70	0.38	**.009**
NFM	**1.18**	0.47, 1.93	0.38	**.002**
SRM	0.20	-0.54, 0.99	0.38	.59
WFM	**0.98**	0.27, 1.78	0.38	**.010**
		Latency ~ Condition + Age + Sex		
Intercept	6.24	5.42, 7.02	0.43	< .001
DRM	**0.98**	0.19, 1.79	0.38	**.010**
NFM	**1.17**	0.44, 1.82	0.38	**.002**
SRM	0.19	-0.47, 0.93	0.38	.61
WFM	**0.97**	0.18, 1.76	0.38	**.011**
Age	-0.03	-0.09, 0.03	0.03	.34
Sex	-0.42	-0.98, 0.14	0.28	.14

Note. DRM = dominant real monkey; NFM = narrow faced model; SRM = subordinate real monkey; WFM = wide faced model.
Significant effects highlighted in bold.

Table 7.2

Latency to approach predicted by contrast for all participants and for adults only

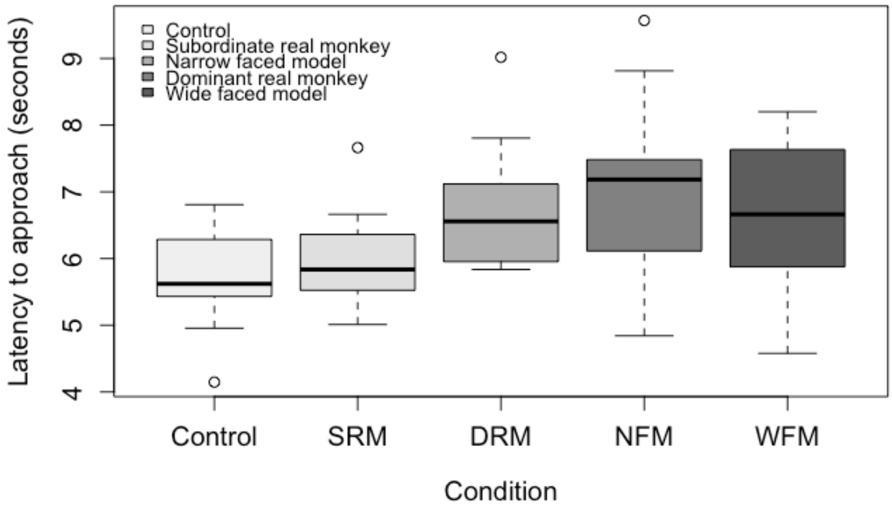
	b	l-95%, u-95% CI	*SE*	*p*
		Latency ~ Contrasts		
Intercept	6.43	6.16, 6.72	0.14	< .001
Baseline/All	**0.67**	0.22, 1.16	0.24	**.005**
Real/Model	0.48	-0.03, 1.04	0.27	.077
NFM/WFM	-0.10	-0.5, 0.26	0.19	.60
SRM/DRM	**0.40**	0.03, 0.82	0.19	**.041**
		Latency ~ Contrasts [Adults only]		
Intercept	6.34	5.96, 6.75	0.21	< .001
Baseline/All	0.53	-0.02, 1.04	0.27	.052
Real/Model	0.17	-0.45, 0.79	0.32	.59
NFM/WFM	0.20	-0.26, 0.66	0.23	.38
SRM/DRM	0.41	-0.04, 0.86	0.23	.073

Note. DRM = dominant real monkey; NFM = narrow faced model; SRM = subordinate real monkey; WFM = wide faced model.
Significant effects highlighted in bold.

7.5 Discussion

7.5.1 Interpretation of results.

The purpose of this study was to assess whether capuchin monkeys perceive differences in face width of conspecifics. We predicted that monkeys would take longer to approach real dominant monkeys over real subordinate monkeys. We also predicted that monkeys would take longer to approach wide faced models over narrow faced models, if they perceived the wide faced models as more dominant. We thus aimed to test whether differences in response to wide vs. narrow faced models reflected differences in response to dominant vs. subordinate conspecifics. Results supported our first prediction. Monkeys took longer to approach dominant members of their group. This supports observations in both the wild and captivity, that rank of conspecifics can influence how individuals respond to them, such as through limiting



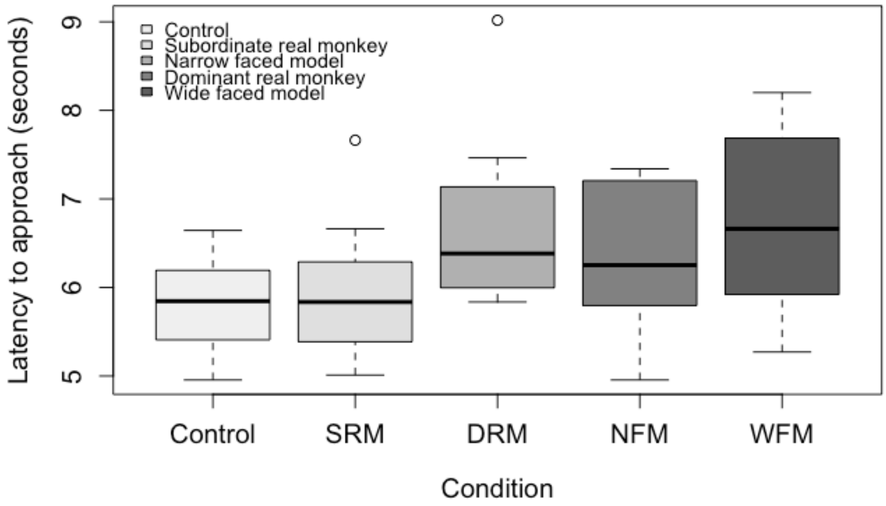


Figure 7.7

Latency to approach in the five different conditions for the full sample (n=14: top plot) and for adults only (n=8: bottom plot). The horizontal line in each box indicates the median latency for that variable. Whiskers indicate minimum and maximum latencies. Control = baseline; SRM = subordinate real monkey; NFM = narrow faced model; DRM = dominant real monkey; WFM = wide faced model.

their proximity to higher ranking group members (Fragaszy et al., 2004; Janson, 1990; Morton et al., 2014).

Although we did not have rank data for the participating monkeys, our results suggest that, on average across the sample, capuchins do differ in their response to group members based on whether they are dominant or not. In contrast to this finding, our second prediction was not supported, that is, the capuchins did not differ significantly in their latency to approach wide versus narrow faced models. This result is surprising, given that face width is associated with both alpha status and assertive traits (Lefevre et al., 2014; Wilson et al., 2014), and also given that the monkeys clearly differ between known conspecifics based on their social status. There are several possible explanations for finding.

One suggestion is that, given the possibility that fWHR is a cue to fighting ability (Lefevre et al., 2014), it is a cue that must either be learned, or simply is of less importance to immature group members and thus, is only salient for mature capuchins who have experience of serious conflict, and the need to avoid it. We must also remember that sexual dimorphism of fWHR only develops at maturity, and furthermore, is associated with alpha status, which can only be gained by fully developed individuals, again suggesting that it is only a relevant cue to adult capuchins. Although we examined effects of adults only in our sample, this sample size was very small and thus lacked the power to find any significant effects.

Another possibility is that fWHR alone does not cue dominance-related traits, but provides a cue in conjunction with proportional body size. As we controlled for body size in our models, it would be worth assessing whether varying body size in relation to fWHR produces differences in approach behaviour. Body weight does correlate with fWHR in brown capuchins, however, body weight does not correlate with Assertiveness, nor does it mediate the relationship between fWHR and Assertiveness (Lefevre et al., 2014). Thus it seems unlikely that body dimensions should add much to the cue of Assertiveness.

An alternative suggestion is that, as proposed by Carré (2014), and similar to suggestions in humans (Goetz et al., 2013; Welker, Goetz, & Carré, 2015), the relationship between Assertiveness and fWHR is driven by non-alpha or low status individuals, and is not significant amongst alpha individuals. Thus, although alpha individuals have wider faces, this theory proposes that alpha faces are not cues to Assertiveness. This opens up the question as to how capuchins perceive wide vs. narrow faces. It is possible that response to facial cues is dependent on the social status of that conspecific (for example a dominant individual with a wide face might pose a different threat compared with a sub-dominant individual with a wide face). However, in the case where individuals meet unfamiliar conspecifics (for example during inter-group migrations in the wild, Janson et al., 2012) they will have no knowledge of the social status of that individual, unless they are able to make that particular judgement from the face alone. Certainly amongst males, the alpha monkey is easy to pick out, even to the human eye, sheerly by his bulky body size and broad face. Thus it is possible that the capuchin face is more a signal of status (i.e. alpha vs. non-alpha) rather than how a general indication of dominance. Recent evidence in macaques supports this idea. Borgi and Majolo (2016) found that fWHR is higher in both sexes in species with despotic female dominance styles, such as in rhesus macaques, compared to more socially tolerant species such as Tonkean macaques. In line with earlier arguments, this implicates face width as being a signal of dominance that obviates the need for conflict amongst species for whom escalated conflict could have serious consequences.

7.5.2 Limitations.

This study has some limitations, which we encourage further research to address. Firstly, our sample was small, which may have led to the lack of significant findings. Replication in a larger sample or across multiple sites could provide some perspective for the current results. There were also several limitations in our design, which should be addressed for future research.

Firstly, the use of the real monkey conditions provided us with a means to assess whether the monkeys' response to familiar conspecifics would differ based on social status of those conspecifics, within our experimental set up. This validated our prediction that, should capuchins perceive wider faces as more dominant, they would be slower to approach this stimulus over approaching a narrow face. However there were several factors we could not control for, meaning that we cannot directly compare latencies between the dominant real monkey condition and wide faced model, or between the subordinate real monkey and narrow faced model. The real monkey condition made use of familiar conspecifics, whilst the model condition used transformed facial image composites of multiple individuals, providing an 'unfamiliar' face. In order to test response to fWHR, it was necessary to use images of an 'unfamiliar' monkey, to avoid response to images being based on social knowledge of a familiar monkey (i.e. through past interactions with that conspecific). To control for differences in response based on familiarity, it would be useful to include two extra conditions, where the model condition is presented with either an image of a familiar alpha or a familiar non-alpha individual.

Our results indicated that monkeys were slower to approach the models versus the real monkeys. Although this is likely due to the unfamiliar facial content of the stimuli (for example, we know that capuchins discriminate between images of their own and other species (Dufour et al., 2006; Pokorny & de Waal, 2009a; 2009b), and that primates in general can recognise conspecifics in images (Bovet & Vauclair, 2000; Dasser, 1987; Marechal, Genty, & Roeder, 2010), we cannot rule out that they were simply responding to the novelty of the model. This could be easily tested by including a 'novel object' condition, such as a model body without facial features or with an inverted face. Previous research has shown that compared to standard face images, inverted or scrambled facial images elicit different responses, such as difficulty in recognition, in some species (see Parr, 2011 for a review).

An additional consideration would be to account for Assertiveness of each participant as a predictor of response to the stimuli. This could also be useful for selecting monkeys for the real monkey condition. We chose monkeys for these conditions based on their social status within the group (i.e. alpha monkey or subadult peripheral male). The use of Assertiveness scores would allow us to select individuals in the upper and lower quartiles of the group, and to ensure these were matched between groups. Although Assertiveness data were collected for this sample previously (Morton, Lee, Buchanan-Smith, et al., 2013), the addition of new juveniles to the group as well as a new alpha male takeover meant that data were either missing or no longer valid for a number of monkeys.

7.5.3 Summary and Future Directions.

Building on our earlier work assessing associations between fWHR and dominance-related traits in brown capuchins (Lefevre et al., 2014; Wilson et al., 2014), in this study we assessed how capuchins perceive differences in fWHR.

Studies in humans have found that people differentiate between faces based on aggression and dominance (Alrajih & Ward, 2013; Lefevre & Lewis, 2013), and that people can perceive personality traits from facial features (Kramer & Ward, 2010; Penton-Voak et al., 2006). This encouraged us to examine similar perceptions in nonhuman primates. The difficulty with translating perceptual studies from humans to nonhumans is the means by which the data are collected. Human research had people provide ratings of facial features (Kramer & Ward, 2010; Penton-Voak et al., 2006), which we cannot do with monkeys, leading us to the difficulty of how to best assess perceptions of facial features in monkeys.

To answer the question posed at the beginning of this chapter 'is the capuchin face a cue to personality?' we can only conclude by saying that the evidence so far suggests not. At the very least, this study provides a methodological step for others to build upon. We encourage further research that assesses facial perceptions in capuchins in a larger sample and with a more robust design, perhaps through the use of video rather than still images of faces to provide a 'realistic' context.

In addition to assessing perceptions of facial morphology, there are still very few studies that assess the relationship of facial morphology with dominance, social status, social tolerance or indeed other personality attributes. Our own research (Lefevre et al., 2014; Wilson et al., 2014) built on the findings of Weston (2004) who first examined sexual dimorphism of bizygomatic face width across a number of species. Despite these findings, and the wealth of research on correlates of fWHR in humans, there is still a lack of research examining these associations in other species, with only one other study since examining fWHR in nonhuman primates (Borgi & Majolo, 2016). One particular aspect that I have not touched on here is the relationship we found between neurotic/attentive traits and face height (Wilson et al., 2014). We proposed that, given the links of Neuroticism and Attentiveness to vigilance and attention in brown capuchins (Morton, Lee, Buchanan-Smith, et al., 2013), lower face/face height could also be linked to social status, perhaps through policing behaviour (Flack, de Waal, & Krakauer, 2005; Flack, Girvan, & de Waal, 2006). This facial metric has primarily been explored in humans in relation to sexual dimorphism (Tanikawa, Zere, & Takada, 2016) facial attractiveness (Feinberg et al., 2005; Penton-Voak et al., 2001) and mate selection (Burriss, Roberts, Welling, Puts, & Little, 2011). Recently, the lower face/face height ratio has also been associated with testosterone in adolescents, and has been found to increase with age in this sample (Hodges-Simeon et al., 2016), reflecting age-related changes that we found in the capuchin monkeys for this metric (Wilson et al., 2014). These findings encourage further examination of lower face/face height in both humans and nonhuman primates. Again, examining whether a similar relationship to personality exists in other species besides capuchins might help us to understand the evolutionary origins of this phenotype.

We have much to learn about how and why personality traits relate to facial morphology, and whether these associations act as signals that can be perceived by conspecifics. Expanding this research to other species could help us understand more about the ancestral origins of social cues in the face, and whether species other than humans can perceive personality from the face.

Chapter 8. Paying Attention to Individual Differences

> "*There is strong evidence that personality does exist in animals. That is, personality ratings… do not merely reflect the implicit theories of observers, projected onto animals*"
>
> - Samuel D. Gosling & Simine Vazire (2002, p. 612)

The purpose of this thesis was to explore the role of personality in the social behaviours of group living primates. Starting by considering the ancestral origins of personality and the role of different selection pressures on shaping species-differences in traits, I then addressed the role of personality directly in social interactions, responses to conspecifics, and in social signals. Assessing four different species over six chapters, I have taken a broad view to understanding how social life has shaped personality, and how personality shapes social lives. Based on the results of these studies I conclude that personality provides a useful approach to understanding how and why individuals differ in their social interactions and perceptions of others. I note that this research has implications for improving welfare of captive primates, and that this is an important reason for understanding more about the origins, diversity and behavioural consequences of personality traits. Below I summarise the main findings of this thesis, and outline the next steps for research in this field.

8.1 Summary

8.1.1 The phylogeny of personality in relation to social structure.

In Chapter 2, I started by considering the ancestral origins of individual differences in primates, by assessing personality structure in Bolivian and common squirrel monkeys, *Saimiri boliviensis* and *S. sciureus*, and examining to what extent similar traits occurred in other primate species. I also considered what differences in selection pressures might have led to trait differences between these two cousins, by comparing their personality structures with that of previously assessed brown capuchins, *Sapajus apella* (Morton, Lee, Buchanan-Smith, et al., 2013). In addition, I assessed the relationship of well-being with personality, as has been done in humans (DeNeve & Cooper, 1998; Steele, Schmidt, & Schulz, 2008), nonhuman apes (King & Landau, 2003; Weiss et al., 2006; Weiss et al., 2009) and Old World monkeys (Weiss et al., 2011).

Both species of squirrel monkey had personality components of Openness, Neuroticism, Assertiveness and Agreeableness. Whilst these structures are similar, Bolivian squirrel monkeys appear to show more similarities to brown capuchins than common squirrel monkeys do, despite the fact that commons share overlapping habitats with capuchins. This suggests that, similar to macaque species (Adams et al., 2015) similarities in social structure between Bolivian squirrel monkeys and capuchins, such as low in-group competition and matrilineal societies, may have led to similarities in personality structure. Alternatively, as brown capuchins and Bolivian squirrel monkeys are phylogenetically closer than capuchins are with common squirrel monkeys (Chiou et al., 2011; Opazo et al., 2006; Schneider & Sampaio, 2015), it is possible that Bolivians simply retain more ancestral traits than common squirrel monkeys. Whilst these comparisons help to illuminate potential selection pressures for personality traits, comparison with other closely related species would be useful to assess whether similarities in social structures are associated with similarities in traits.

Both squirrel monkey species share a similar structure of Neuroticism and Agreeableness components, suggesting that these traits may be derived within the *Saimiri* genus. However, between-species comparisons revealed that each showed more similarity with capuchins than with each other for components Openness and Assertiveness. Similar to recent research assessing differences between chimpanzees and bonobos (Weiss et al., 2015), such comparisons between closely related species help to highlight how personality has diverged across primate taxa, and also expand our knowledge of personality to a wider genera (Freeman & Gosling, 2010).

Finally, in Chapter 2 I also explored the relationship of well-being to personality in both species of squirrel monkey. Whilst results in common squirrel monkeys were limited by sample size, in Bolivian squirrel monkeys, well-being was correlated negatively with Neuroticism and positively with Openness, consistent with findings in apes and rhesus macaques (Weiss et al., 2006; Weiss et al., 2009; Weiss et al., 2011) and in felids (Gartner, Powell & Weiss, 2016). These findings suggest that the relationship of well-being to specific personality traits is potentially ancient, at the very least predating the split of Old World and New World monkeys 43 mya (Steiper & Young, 2006). Understanding the relationship of well-being to personality is important for understanding why individuals differ in their ability to cope with stress or emotionally challenging situations, and what traits might put individuals at risk of reduced well-being.

These are important considerations in addressing the welfare of captive animals, particularly in large groups where individual needs and coping mechanisms may vary.

8.1.2 Personality predicts atypical behaviour and social response.

In Chapters 3 and 4 I considered the role of personality in welfare through the assessment of autistic-like traits in chimpanzees. These chapters addressed whether atypical behaviour, which has parallels between humans and nonhuman primates (Clay et al., 2015; Emerson et al., 2001; Goldman et al., 2009; Suomi & Harlow, 1972), may have originated in the social complexity of primate group life (Dunbar, 2013), and suggest that chimpanzees exhibit personality types – subordinate, introverted and emotionally unstable - consistent with traits associated with autism. For example, items such as excitable, anxious and solitary, which characterise high autism scores in chimpanzees, may also be associated with the behaviour of a person with autism (DSM-V: APA, 2013; Baron-Cohen & Belmonte, 2005). The purpose of this research was not to suggest that chimpanzees have autism, or that autism is a condition that can be applied to nonhuman species. Rather, we wished to explore to what extent chimpanzees exhibited traits seen in autistic individuals by calculating autism scores, and if these traits related to deficiencies in social behaviour or higher prevalence of stereotypical behaviours. In fact, we found that personality was, overall, a better predictor of social and stereotypical behaviours in chimpanzees, suggesting that our measure of autistic-like traits did not reflect any underlying neurodevelopmental issues. Instead, we suggest that autism scores in chimpanzees are more representative of a certain type of personality, which may instead be an underlying precursor to atypical behaviour.

In Chapter 4, we noted that Neuroticism was, tentatively, a predictor of regurgitation behaviour, a link that should be explored further, particularly in regard to other stereotypies. Are chimpanzees that exhibit neurotic traits at higher risk of stress? Or do they have different coping mechanisms to difficult environments than other chimpanzees? It would be interesting to compare how, amongst rehabilitating chimpanzees, individuals differing in Extraversion and Neuroticism vary in how they adapt to a change in environment. In this study we also found that neurotic individuals tended to receive grooming more than they gave grooming, whilst extraverted individuals were more likely to groom others than be groomed. Grooming is a socially important behaviour that strengthens social bonds (Crockford et al., 2013). Grooming networks also shrink in response to stress (Wittig et al., 2008). That personality is associated with direction of grooming suggests that individuals high in Neuroticism and Extraversion may benefit differently from grooming relationships, through mechanisms that mediate either social networking or stress release. Of interest here could be the study of links between personality and neuropeptide release in social situations, for example measuring oxytocin release in relation to personality following grooming (Crockford et al., 2013). Such studies could help to elucidate the processes by which individual differences impact on welfare.

One way of understanding the role of personality in social contexts is to assess how chimpanzees differ in their response to emotional events. This is the question I focused on in Chapter 5, by exploring individual differences in responsiveness to emotional events in conspecifics. Responsiveness for all events was negatively related to Openness. Responsiveness for events pertaining to submissive barks was positively associated with Extraversion, and negatively associated with Dominance, Agreeableness and Neuroticism.

Examining the types of behaviours exhibited as a response, we found four components of response, three of which were related to personality – Look, Move and Arousal. Looking behaviour is thought to be a measure of social attention (Kano & Tomonaga, 2010; McNelis & Boatright-Horowitz, 1998; Seyfarth, Cheney & Bergman, 2005; von Rohr et al., 2015). Thus we took 'Look' to indicate attention to events, which seems to occur in the absence of Move or Arousal, and is characterised by its positive relationship to Neuroticism. Moving in response to conflict was negatively related to Neuroticism, and positively associated with Openness, indicating that chimpanzees high in Openness appear to be interested in conflict. Look and Move were furthermore significantly negatively related. The fact that they both have distinct, different relationships to personality suggests that both may be a measure of attentiveness and awareness of emotional events in others, but do not tend to occur simultaneously.

The Arousal component comprised swaying and hooting behaviours, which are typically associated with displays (Coe & Levin, 1980). Arousal responses were also most strongly (though not statistically significantly) associated with Hoots events amongst conspecifics, which is indicative of emotional contagion (Hatfield et al., 1994). Arousal was not significantly related to either Look or Move. This supports the argument for separate levels of emotional perception, suggesting that arousal occurs relatively independently of attention-based responses (de Waal, 2008). Chimpanzees higher in Agreeableness, Dominance and Neuroticism showed higher Arousal overall, indicating that several variables, relating to sensitivity, excitability and possibly rank could all play a role in how easily aroused a chimpanzee can become.

In addition to examining responses to events within the chimpanzees' social group, I also examined whether chimpanzees demonstrated cognitive empathy, by measuring their looking time as a response to video footage of social scenario outcomes. Chimpanzees looked longer at the outcome which contained emotional stimuli of negative valence, rather than the outcome which should have violated their expectations. The most likely explanation for this is that chimpanzees simply find the emotional outcome more arousing and, consistent with earlier findings (Kano & Tomonaga, 2010), are responding to the emotional content, rather than relating the outcome to the prior scenario. This does not mean that they do not form expectations of how individuals should respond to being the victim of aggression. Rather, it is possible that they did not perceive a causal link between the different scenes, and thus cannot perceive a neutral outcome as surprising if they have no expectations. It is also possible that they did follow the footage, but do not tend to form social expectations based on conflict outcomes and thus, find neither outcome surprising. Although these results provide no evidence of cognitive empathy in chimpanzees, as yet, it cannot be ruled out. Instead, this study raises questions about the methodology that can be used to test chimpanzees' perceptions of others' emotions.

The primary finding of interest of the experiment was that, similar to looking behaviour in the group environment, looking time to the outcomes was positively associated with Neuroticism. Whilst this suggests that there may be consistency in responses across contexts, we found no link between responsiveness or looking behaviour in the group environment with looking time to the video outcomes. This suggests that responses to different emotional stimuli are not consistent. However, we used different measures of response between the behavioural and experimental contexts; we also did not account for event type in our analyses. The relationship between personality and response type can vary with the type of event, be it conflict, display or submissive barks. Thus without examining event context or using comparable measures between studies, it seems premature to conclude that responses to emotional stimuli are not consistent across contexts with different stimuli.

8.1.3 Traits as social signals.

So far, these results suggest that an individual's personality influences how they respond to conspecifics, at least in chimpanzees. I was also interested in examining the opposite relationship, that is, how do individuals respond to different traits in conspecifics, such as dominance? The first step in this research was examining morphological measures of personality in the faces of brown capuchins. In Chapter 6, I report a positive relationship between fWHR and Assertiveness, and a relationship of lower face/face height to Neuroticism (positively) and Attentiveness (negatively) (Lefevre et al., 2014; Wilson et al., 2014). Considering that the face is such an important tool for communication (De Marco et al., 2008; Emery, 2000; Visalberghi et al., 2006), it is possible that the face acts as a signal of certain traits, allowing other monkeys to 'read' the faces of conspecifics. For example, fWHR could signal combat ability through links to bite strength or skull strength (Lefevre et al., 2014), Alternatively, facial morphology could be a signal of fitness in mate choice (Burriss et al., 2011; Valentine et al., 2014).

In Chapter 7 we aimed to test whether the face is a signal of dominance by assessing how capuchins respond to faces of 'unfamiliar' conspecifics with different widths, and familiar conspecifics of different social rank. As predicted, they were slower to approach familiar alpha monkeys than they were to approach a subordinate member of their group. Thus, knowledge of social rank clearly affects individual response to conspecifics, consistent with previous observations (Fragaszy et al., 2004; Janson, 1990; Morton et al., 2014). We expected that the monkeys would also be slower to approach the wide faced model (unfamiliar) condition, because wider faces are associated with more assertive traits. In fact, they were slower to approach the narrow faced model. We discussed a number of possibilities as to why this could be. fWHR may be a learned cue, which could explain why the direction of the effect was reversed when we excluded juveniles from the sample. One possibility is that facial cues are primarily a signal of status rather than of behaviour. It is possible that in conjunction with body size, this provides a cue to whether that individual has an alpha position or not, a relationship that may be driven by non-alpha individuals rather than alpha individuals (Goetz et al., 2013).

Thus, although capuchins evidently differentiate between conspecifics based on social status, it is not clear that they differentiate based on morphological features that reflect differences in assertive traits. In humans, studies of fWHR and broader facial measures are generally in agreement that humans can perceive differences in facial features and correctly attribute particular traits associated with these features (Alrajih & Ward, 2013; Kramer & Ward, 2010; Mileva et al., 2014; Lefevre & Lewis, 2013; Penton-Voak et al., 2006). Thus, it is possible that such perceptions exist in other species, especially given the similarities in face width and dominance-linked traits in both humans (Trebicky et al., 2015; Zilioli et al., 2014), capuchins (Lefevre et al., 2014; Wilson et al., 2014) and macaques (Borgi & Majolo, 2016).

One further area that we did not address was the link between face height and Neuroticism. This association has not been explored in humans; the finding in capuchins is currently the only report of this link. Studying whether similar associations exist in other primate species, particularly in humans, could be useful in understanding links between face height and neurotic traits in brown capuchins. It is possible that lower face/face height is also a form of status signaling (Wilson et al., 2014), linked to vigilant behaviour and social monitoring (Flack et al., 2006; Morton et al., 2013) rather than dominance. Examining face height, neurotic and attentive traits in individuals of different social rank could be an additional way of addressing whether face height has any links to status, and could establish whether it also has the potential to be a social signal.

8.2 Critical evaluation

The scope of this thesis in examining personality in different species and contexts has allowed me to consider the role of personality in a broad sense, for example, through examining trait-structural differences across phylogeny, or through addressing the relationship between personality traits and perception of emotions and faces. I believe this cross-species approach to be a strength of this thesis, in particular, through addressing personality in two species of South American squirrel monkey (Chapter 2), I have expanded the focus of personality assessment to include a broader taxa. Moreover, by using a multi-method approach, through incorporating questionnaire ratings, behavioural observation and experiments into my methodology, I have addressed not only broad-set personality dimensions but also the context-specific associations of these traits, such as individual differences in chimpanzee emotional perception (Chapter 5). In particular, the latency-to-approach design laid out in Chapters 6 and 7 presents a simple but effective way to test response to social stimuli in brown capuchins, by using approach to dominant conspecifics as a measure to understand approach to novel facial stimuli. Furthermore, by assessing personality in relation to social and stereotypic behaviour in Chapter 4, I consider how assessing individual differences in these behaviours could benefit our understanding and treatment of welfare issues in captive chimpanzees.

There are however some limitations of the approach I take in this thesis. Focusing on one or two species would have allowed me to study them in more detail, and perhaps to have expanded the methodology within these species. For example, in chimpanzees, further experimental work could try to disentangle social expectation from emotional interest, and could also consider responses to positive emotion (Chapter 5). An additional constraint was sample size – in common squirrel monkeys, the subjective well-being ratings were too few to reveal any relationship to personality; furthermore, the sample size for both species of squirrel monkey mean that we should be cautious in how we extrapolate these findings to each species as a whole. In brown capuchins, a larger sample of adults would have benefited our understanding of their responses to wide versus narrow faced stimuli; and in chimpanzees, having all 18 individuals participate in experimental testing could have bolstered our understanding of looking behaviour to emotional stimuli across contexts. Finally, whilst personality provides a useful measure by which to understand individual differences across context, in all of these studies we were unable to control for developmental and rearing history of the participating species groups. Thus, we cannot say to what extent behavioural outcomes might be influenced by early life environment versus inherited traits (for example in Chapter 3). This is an important point that should be given careful consideration in future studies, especially with regard to understanding atypical behaviour.

8.3 Future directions

In sum, this thesis highlights the importance of personality in shaping social relationships and responses to others, as well as the potential role of social structure in shaping particular personality traits between species. Understanding how personality evolved and diverged across taxa may help us to better understand how the relationship between well-being and personality evolved, and why personality plays such an important role in social interactions. These findings should help to pave the way for future, more focused research that allows us to understand in detail the nature of the relationships between individual traits and social perceptions and interactions.

There are numerous ways in which we can build on this understanding. For example, examining the neural (Kanske et al., 2015; Moore et al., 2015), genetic (Bouchard & Loehlin, 2001; Inoue-Murayama, 2009; van Oers et al., 2005) and hormonal (Bielsky et al., 2004; Rilling et al., 2012) basis of particular traits or behaviours could help us identify to what extent variance in social behaviour is determined by innate versus environmental variables. Continuing to compare personality traits between species with differing social structures could also allow us to examine in more detail whether, and how, social structures act as a selection for particular traits.

The assessment of well-being, in relation to both personality and to particular welfare measures such as stereotypies and social behaviour, provides an important step in improving knowledge and management of captive care procedures. Knowing which individuals are at risk of low well-being and being able to identify particular markers that could indicate that risk could prove useful to improving individual welfare. As personality seems to be linked to atypical behaviour in chimpanzees, studying this further by examining whether neurotic traits predict stereotypies other than regurgitation, could also benefit our understanding of the origins of stereotypies in humans.

Further experimental work utilizing larger sample sizes could illuminate how personality affects perception of and attention to social and emotional stimuli. A more robust testing procedure is needed to ascertain whether chimpanzees can understand emotional perspectives, for example, by expanding assessment beyond just looking time to emotional stimuli to the use of thermal imaging (Kuraoka & Nakamura, 2011; Kano et al., 2016), eye tracking (Kano & Tomonago, 2009), heart rate measures (Berntson et al., 1989; Parr & Hopkins, 2000) or response time to emotional stimuli (Kret, Jaasma, Bionda, & Wijnen, 2016; Lacreuse, Schatz, Strazzullo, King, & Ready, 2013). Similar procedures could help us understand how individuals respond to different types of traits, and whether they perceive morphological features as signals of these traits. In particular, examining links between personality and facial morphology in other species, perhaps accounting for social structure and social tolerance/agonism, could help us understand the role of face width in conflict and trait signaling.

Further attention should also be given to the link between face height and neurotic and attentive traits, examining whether such associations also exist in other species.

Taken together, the chapters of this thesis contribute novel empirical findings to the growing field of personality, and present multiple avenues of further research. It is now difficult to deny that animals, like humans, have personalities, which can be reliably assessed using item ratings, quantified, and considered in relation to species, behaviour and well-being. The increasing acceptance of personality research in nonhuman primates provides the opportunity to address the role of individual differences within social-group contexts, and to consider how personality, social structure and social interactions shape each other.

References

Adams, M. J., Majolo, B., Ostner, J., Schulke, O., De Marco, A., Thierry, B., . . . Weiss, A. (2015). Personality structure and social style in macaques. *Journal of Personality and Social Psychology, 109*(2), 338-353. doi: 10.1037/pspp0000041

Alfaro, J. W. L., de Sousa Silva, J., & Rylands, A. B. (2012). How different are robust and gracile capuchin monkeys? An argument for the use of *Sapajus* and *Cebus*. *American Journal of Primatology*, *74*(4), 273-286.

Allport, G. D., & Odbert, H. S. (1936). Trait-Names. A Psycho-lexical study. *Psychological Review Publications, 47*(211), 1-171.

Alrajih, S., & Ward, J. (2014). Increased facial width-to-height ratio and perceived dominance in the faces of the UK's leading business leaders. *Br J Psychol, 105*(2), 153-161. doi: 10.1111/bjop.12035

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, *49*(3), 227-266.

Altschul, D. M., Terrace, H. S., & Weiss, A. (2016). Serial cognition and personality in macaques. *Animal Behavior and Cognition, 31*(1), 46-64.

American Psychiatric Association (2000). *The Diagnostic and statistical manual of mental disorders (DSM-IV-TR)*. Washington, DC: American Psychriatric Publishing.

American Psychiatric Association (2013). *The Diagnostic and statistical manual of mental disorders (DSM-5®)*. Washington, DC: American Psychiatric Publishing.

Anderson, J. R., Myowa-Yamakoshi, M., & Matsuzawa, T. (2004). Contagious yawning in chimpanzees. *Proc Biol Sci, 271 Suppl 6*, S468-470. doi: 10.1098/rsbl.2004.0224

Anestis, S. F., Webster, T. H., Kamilar, J. M., Fontenot, M. B., Watts, D. P., & Bradley, B. J. (2014). AVPR1A variation in chimpanzees (*Pan troglodytes*): Population differences and association with behavioral style. *International Journal of Primatology, 35*(1), 305-324. doi: 10.1007/s10764-013-9747-z

Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., ... & Holekamp, K. (2008). Fission-fusion dynamics. *Current Anthropology*, *49*(4), 627-654.

Bachner-Melman, R., Zohar, A. H., Bacon-Shnoor, N., Elizur, Y., Nemanov, L., Gritsenko, I., & Ebstein, R. P. (2005). Link between vasopressin receptor AVPR1A promoter region microsatellites and measures of social behavior in humans. *Journal of Individual Differences, 26*(1), 2-10. doi: 10.1027/1614-0001.26.1.2

Bachrach, Y., Kosinski, M., Graepel, T., Kohli, P., & Stillwell, D. (2012). Personality and patterns of Facebook usage. In *Proceedings of the 4th Annual ACM Web Science Conference*.

Bard, K. (1998). Social-experiential contributions to imitation and emotion in chimpanzees. In S. Bråten (Ed.), *Intersubjective Communication and Emotion in Early Ontogeny*, (pp. 208-227). Cambridge, UK: Cambridge University Press.

Bard, K. A., Brent, L., Lester, B., Worobey, J., & Suomi, S. J. (2011). Neurobehavioral integrity of chimpanzee newborns: Comparisons across groups and across species reveal gene-environment interaction effects. *Infant Child Development, 20*(1), 47-93. doi: 10.1002/icd.686

Bard, K. A., Dunbar, S., Maguire-Herring, V., Veira, Y., Hayes, K. G., & McDonald, K. (2014). Gestures and social-emotional communicative development in chimpanzee infants. *American Journal of Primatology*, *76*(1), 14-29.

Bard, K. A., & Leavens, D. A. (2009). Socio-emotional factors in the development of joint attention in human and ape infants. In: L. S. Röska-Hardy & E. M. Neumann-Held (Eds.), *Learning from animals? Examining the nature of human uniqueness*, (pp. 89-104). Hove, UK: Psychology Press.

Barenbaum, N. B., & Winter, D. G. (2008). History of Modern Personality Theory and Research. In O. P. John, R. W. Robins & L. A. Pervin (Eds.), *Handbook of Personality: Theory and Research,* (pp. 3-26). New York, USA: Guilford Press.

Barlow, C. J. C., Caldwell, C. A., & Lee, P. C. (2006). *Individual differences and reactions to visitors in zoo-housed Diana monkeys*. Paper presented at the Annual symposium on zoo research, Colchester Zoo.

Baron-Cohen, S. (2001). Theory of mind and autism: A review. *International review of research in mental retardation: Autism, 23*(169-184).

Baron-Cohen, S. (2002). The extreme male brain theory of autism. *Trends in Cognitive Sciences, 6*, 248-254.

Baron-Cohen, S., & Belmonte, M. K. (2005). Autism: A window onto the development of the social and the analytic brain. *Annual Review of Neuroscience, 28*, 109-126. doi: 10.1146/

Baron-Cohen, S., Leslie, A. M., & Frith, U. (1985). Does the autistic child have a "theory of mind"? *Cognition, 21*(1), 27-46.

Baron-Cohen, S., & Wheelwright, S. (2004). The empathy quotient: an investigation of adults with Asperger syndrome or high functioning autism, and normal sex differences. *Journal of Autism and Developmental Disorders*, *34*(2), 163-175.

Baron-Cohen, S., Wheelwright, S., Skinner, R., Martin, J., & Clubley, E. (2001). The Autism-Spectrum Quotient (AQ): Evidence from Asperger Syndrome/High-Functioning Autism, Males and Females, Scientists and Mathematicians. *Journal of Autism and Developmental Disorders, 31*(1), 5-17.

Barrio, V. D., Aluja, A., & García, L. F. (2004). Relationship between empathy and the Big Five personality traits in a sample of Spanish adolescents. *Social Behavior and Personality: an international journal*, *32*(7), 677-681.

Bartels, M. (2015). Genetics of wellbeing and its components satisfaction with life, happiness, and quality of life: a review and meta-analysis of heritability studies. *Behavior genetics*, *45*(2), 137-156.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software, 67*(1), 1-48. doi:10.18637/jss.v067.i01.

Berglund, A., Bisazza, A., & Pilastro, A. (1996). Armaments and ornaments: an evolutionary explanation of traits of dual utility. *Biological Journal of the*

Linnean Society, *58*(4), 385-399.

Bergman, T. J., Ho, L., & Beehner, J. C. (2009). Chest color and social status in male geladas (*Theropithecus gelada*). *International Journal of Primatology*, *30*(6), 791-806.

Bergman, T. J., & Sheehan, M. J. (2013). Social knowledge and signals in primates. *American Journal of Primatology*, *75*(7), 683-694.

Berntson, G. G., Boysen, S. T., Bauer, H. R., & Torello, M. S. (1989). Conspecific screams and laughter: Cardiac and behavioral reactions of infant chimpanzees. *Developmental Psychobiology, 22*(8), 771-787.

BIAZA (2016). Our Vison and Misson, from http://www.biaza.org.uk/about-biaza/our-vision/

Bielsky, I. F., Hu, S. B., Szegda, K. L., Westphal, H., & Young, L. J. (2004). Profound impairment in social recognition and reduction in anxiety-like behavior in vasopressin V1a receptor knockout mice. *Neuropsychopharmacology, 29*(3), 483-493. doi: 10.1038/sj.npp.1300360

Birkett, L. P., & Newton-Fisher, N. E. (2011). How abnormal is the behaviour of captive, zoo-living chimpanzees? *PloS ONE*, *6*(6), e201rzss01.

Bloomsmith M., Baker K., Ross S., & Lambeth, S. (2005). Early rearing conditions and captive chimpanzee behavior: some surprising findings. In: G. Sackett & G. Ruppenthal (Eds.), *Nursery rearing of nonhuman primates in the 21st century,* (pp. 289-312). New York, USA: Kluver Academic Publishers.

Bloomsmith, M. A., Lambeth, S. P., & Alford, P. L. (1990). The Relationship between social behavior and genital swelling in captive female chimpanzees: Implications for managing chimpanzee (*Pan troglodytes*) groups. *International Journal of Comparative Psychology*, *4*(2), 171-185.

Boinski, S., & Cropp, S. J. (1999). Disparate data sets resolve squirrel monkey (*Saimiri*) taxonomy: implications for behavioral ecology and biomedical usage. *International Journal of Primatology, 20*(2), 237-256.

Boinski, S., Kauffman, L., Ehmke, E., Schet, S., & Vreedzaam, A. (2005). Dispersal patterns among three species of squirrel monkeys (*Saimiri oerstedii, S. boliviensis* and *S. sciureus*): I. Divergent costs and benefits. *Behaviour 142*(5), 525-632. doi: 10.1163/1568539054352888

Boinski, S., Sughrue, K., Selvaggi, L., Quatrone, R., Henry, M., & Cropp, S. (2002). An expanded test of the ecological model of primate social evolution: Competitive regimes and female bonding in three species of squirrel monkeys (*Saimiri oerstedii, S. boliviensis*, and *S. sciureus*). *Behaviour, 139*(2/3), 227-261.

Borgi, M., & Majolo, B. (2016). Facial width-to-height ratio relates to dominance style in the genus *Macaca*. *PeerJ*, *4*, e1775.

Bouchard Jr., T. J., & Loehlin, J. C. (2001). Genes, evolution, personality. *Behavior Genetics, 31*(3), 243-273.

Bovet, D., & Vauclair, J. (2000). Picture recognition in animals and humans. *Behavioural brain research*, *109*(2), 143-165.

Bräuer, J., Call, J., & Tomasello, M. (2009). Are apes inequity averse? New data on the token-exchange paradigm. *American Journal of Primatology, 71*(2), 175-181.

Briefer, E. F., Oxley, J. A., & McElligott, A. G. (2015). Autonomic nervous system reactivity in a free-ranging mammal: effects of dominance rank and personality. *Animal Behaviour, 110*, 121-132. doi: 10.1016/j.anbehav.2015.09.022

Broom, D. M. (1991). Animal welfare: concepts and measurement. *Journal of Animal Science*, *69*(10), 4167-4175.

Brown, T. A., Sautter, J. A., Littvay, L., Sautter, A. C., & Bearnes, B. (2010). Ethics and personality: Empathy and narcissism as moderators of ethical decision making in business students. *Journal of Education for Business*, *85*(4), 203-208.

Brüne, M., Brüne-Cohrs, U., McGrew, W. C., & Preuschoft, S. (2006). Psychopathology in great apes: concepts, treatment options and possible homologies to human psychiatric disorders. *Neuroscience & Biobehavioral Reviews*, *30*(8), 1246-1259.

Bugnyar, T., & Kotrschal, K. (2004). Leading a conspecific away from food in ravens (Corvus corax)? *Animal Cognition, 7*(2), 69-76. doi: 10.1007/s10071-003-0189-4

Burriss, R. P., Roberts, S. C., Welling, L. L., Puts, D. A., & Little, A. C. (2011). Heterosexual romantic couples mate assortatively for facial symmetry, but not masculinity. *Personality and Social Psychology Bulletin*, *37*(5), 601-613.

Butterworth, G., & Jarrett, N. (1991). What minds have in common is space: Spatial mechanisms serving joint visual attention in infancy. *British Journal of Developmental Psychology, 9*(1), 55-72.

Caldwell, H. K., Lee, H. J., Macbeth, A. H., & Young Ill, W. S. (2008). Vasopressin: Behavioral roles of an “original” neuropeptide. *Progress in Neurobiology, 84*(1), 1-24.

Call, J., & Tomasello, M. (2008). Does the chimpanzee have a theory of mind? 30 years later. *Trends in Cognitive Science, 12*(5), 187-192. doi: 10.1016/j.tics.2008.02.010

Capitanio, J. P. (1999). Personality dimensions in adult male rhesus macaques: Prediction of behaviors across time and situation. *American Journal of Primatology, 47*, 299-320.

Capitanio, J. P., Abel, K., Mendoza, S. P., Blozis, S. A., McChesney, M. B., Cole, S. W., & Mason, W. A. (2008). Personality and serotonin transporter genotype interact with social context to affect immunity and viral set-point in simian immunodeficiency virus disease. *Brain Behav Immun, 22*(5), 676-689. doi: 10.1016/j.bbi.2007.05.006

Capitanio, J. P., & Widaman, K. F. (2005). Confirmatory factor analysis of personality structure in adult male rhesus monkeys (*Macaca mulatta*). *American Journal of Primatology, 65*(3), 289-294. doi: 10.1002/ajp.20116

Carlstead, K., Fraser, J., Bennet, C., & Leiman, D. G. (1999). Black rhinoceros (*Diceros bicornis*) in U.S. zoos: II. behavior, breeding success, and mortality in relation to housing facilities. *Zoo Biology, 18*(1), 35-52.

Carpenter, M., Nagell, K., Tomasello, M., Butterworth, G., & Moore, C. (1998). Social cognition, joint attention, and communicative competence from 9 to 15 months of age. *Monographs of the society for research in child development, 63*(4), i-174.

Carré, J. M. (2014). Social status, facial structure, and assertiveness in brown capuchin monkeys. *Frontiers in psychology*, *5*, 1-3.

Carré, J. M., & McCormick, C. M. (2008). In your face: facial metrics predict aggressive behaviour in the laboratory and in varsity and professional hockey players. *Proceedings of the Royal Society B: Biological Sciences, 275*(1651), 2651-2656.

Carré, J. M., McCormick, C. M., & Mondloch, C. J. (2009). Facial structure is a reliable cue of aggressive behavior. *Psychological Science*, *20*(10), 1194-1198.

Catell, R. B. (1945). The description of personality: Principles and findings in a factor analysis. *The American Journal of Psychology, 58*(1), 69-90.

Chabris, C. F., Hebert, B. M., Benjamin, D. J., Beauchamp, J., Cesarini, D., van der Loos, M., . . . Laibson, D. (2012). Most reported genetic associations with general intelligence are probably false positives. *Psychological Science, 23*(11), 1314-1323. doi: 10.1177/0956797611435528

Chapman, C. A., & Lefebvre, L. (1990). Manipulating foraging group size: spider monkey food calls at fruiting trees. *Animal Behaviour, 39*, 891-896.

Cheney, D. L., Seyfarth, R. M., & Silk, J. B. (1995). The responses of female baboons (Papio cynocephalus ursinus) to anomalous social interactions: evidence for causal reasoning? *Journal of Comparative Psychology*, *109*(2), 134-141.

Cheney, D. L., Seyfarth, R. M., & Silk, J. B. (1995). The responses of female baboons (*Papio cynocephalus ursinus*) to anomalous social interactions: Evidence for causal reasoning? . *Journal of Comparative Psychology, 109*(2), 134-141.

Chiou, K. L., Pozzi, L., Lynch Alfaro, J. W., & Di Fiore, A. (2011). Pleistocene diversification of living squirrel monkeys (*Saimiri* spp.) inferred from complete mitochondrial genome sequences. *Molecular Phylogenetics and Evolution, 59*(3), 736-745. doi: 10.1016/j.ympev.2011.03.025

Clay, A. W., Bloomsmith, M. A., Bard, K. A., Maple, T. L., & Marr, M. J. (2015). Long-term effects of infant attachment organization on adult behavior and health in nursery-reared, captive chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *129*(2), 145.

Coe, C. L., & Levin, R. N. (1980). Dominance assertion in male chimpanzees (*Pan troglodytes*). *Aggressive Behavior*, *6*(2), 161-174.

Costa, P. T., & McCrae, R. R. (1992). Four ways five factors are basic. *Personality and individual differences*, *13*(6), 653-665.

Costa, P. T., McCrae, R. R., & Dye, D. A. (1991). Facet scales for agreeableness and conscientiousness:a revision of the NEO Personality Inventory. *Personality and Individual Differences, 12*(9), 887-898.

Crawford, M. P. (1938). A behaviour rating scale for young chimpanzees. *Journal of Comparative Psychology, 26*(1), 79-92.

Crockford, C., Wittig, R. M., Langergraber, K., Ziegler, T. E., Zuberbühler, K., & Deschner, T. (2013). Urinary oxytocin and social bonding in related and unrelated wild chimpanzees. *Proceedings of the Royal Society of London B: Biological Sciences*, *280*(1755), 20122765.

Crockford, C., Wittig, R. M., Mundry, R., & Zuberbuhler, K. (2012). Wild chimpanzees inform ignorant group members of danger. *Current Biology, 22*(2), 142-146. doi: 10.1016/j.cub.2011.11.053

Crockford, C., Wittig, R. M., Whitten, P. L., Seyfarth, R. M., & Cheney, D. L. (2008). Social stressors and coping mechanisms in wild female baboons (*Papio hamadryas ursinus*). *Hormones and Behavior*, *53*(1), 254-265.

Dabbs, J., & Hargrove, M. F. (1997). Age, testosterone, and behavior among female prison inmates. *Psychosomatic Medicine*, *59*(5), 477-480.

Dasser, V. (1987). Slides of group members as representations of the real animals (*Macaca fascicularis*). *Ethology*, *76*(1), 65-73.

Dapretto, M., Davies, M. S., Pfeifer, J. H., Scott, A. A., Sigman, M., Bookheimer, S. Y., & Iacoboni, M. (2006). Understanding emotions in others: mirror neuron dysfunction in children with autism spectrum disorders. *Nature Neuroscience, 9*(1), 28-30. doi: 10.1038/nn1611

Davenport, R. K., & Menzel, E. W. (1963). Stereotyped behavior of the infant chimpanzee. *Archives of General Psychiatry, 8*, 99-120.

Darwin, C. (1872). *The origin of species, 6th edition*. Chicago, IL: Thompson and Thomas.

Davis, M. H. (1980). A multidimensional approach to individual differences in empathy. *JSAS Catalog of Selected Documents in Psychology, 10,* 1-19.

Davis, M. H., Mitchell, K. V., Hall, J. A., Lothert, J., Snapp, T., & Meyer, M. (1999). Empathy, expectations, and situational preferences: Personality influences on the decision to participate in volunteer helping behaviors. *Journal of personality*, *67*(3), 469-503.

Dawkins, R. & Krebs, J. J. (1978). Animal signals: information or manipulation? In J.R. Krebs and N.B. Davies (Eds.), *Behavioural ecology: an evolutionary approach, 1st edition,* (pp. 282-309). Oxford, UK: Blackwell Scientific Publications.

D'eath, R. B. (1998). Can video images imitate real stimuli in animal behaviour experiments? *Biological Reviews*, *73*(3), 267-292.

De Rouck, M., Kitchener, A. C., Law, G., & Nelissen, M. (2005). A comparative study of the influence of social housing conditions on the behaviour of captive tigers (*Panthera tigris*). *Animal Welfare, 14*, 229-238.

de Waal, F. B. (1996). *Good Natured: The Origins of Right and Wrong in Humans and Other Animals*. Cambridge, MA: Harvard University Press.

de Waal, F. B. (2008). Putting the altruism back into altruism: the evolution of empathy. *Annu Rev Psychol, 59*, 279-300. doi: 10.1146/annurev.psych.59.103006.093625

de Waal, F. B., & Aureli, F. (1996). Consolation, reconciliation, and a possible cognitive difference between macaques and chimpanzees. In A. E. Russon, K. A. Bard & S. T. Parker (Eds.), *Reaching into thought: The minds of the great apes*, (pp. 80-110). Cambridge, UK: Cambridge University Press.

de Waal, F. B., & van Roosmalen, A. (1979). Reconciliation and consolation among chimpanzees. *Behavioral Ecology and Sociobiology*, *5*(1), 55-66.

Deaner, R. O., Goetz, S. M., Shattuck, K., & Schnotala, T. (2012). Body weight, not facial width-to-height ratio, predicts aggression in pro hockey players. *Journal of Research in Personality, 46*(2), 235-238.

Deary, I. J., Weiss, A., & Batty, G. D. (2010). Intelligence and personality as predictors of illness and death: How researchers in Differential Psychology and Chronic Disease Epidemiology are collaborating to understand and address health inequalities. *Psychological Science in the Public Interest, 11*(2), 53-79. doi: 10.1177/1529100610387081

Decety, J., & Jackson, P. L. (2004). The functional architecture of human empathy. *Behavioural and Cognitive Neuroscience Reviews, 3*(2), 71-100. doi: 10.1177/1534582304267187

DeNeve, K. M., & Cooper, H. (1998). The happy personality: a meta-analysis of 137 personality traits and subjective well-being. *Psychological Bulletin, 124*(2), 197.

De Marco, A., Petit, O., & Visalberghi, E. (2008). The repertoire and social function of facial displays in *Cebus capucinus*. *International Journal of Primatology*, *29*(2), 469-486.

Descovich, K. A., Galdikas, B. M., Tribe, A., Lisle, A., & Phillips, C. J. (2011). Fostering appropriate behavior in rehabilitant orangutans (*Pongo pygmaeus*). *International Journal of Primatology, 32*(3), 616-633. doi: 10.1007/s10764-011-9491-1

Dethier, V. G. (1964). Microscopic Brain. *Science, 143*(1138-1145).

DeYoung, C. G., Quilty, L. C., Peterson, J. B., & Gray, J. R. (2014). Openness to experience, intellect, and cognitive ability. *Journal of Personality Assessment, 96*(1), 46-52.

Di Bitetti, M. S. (1997). Evidence for an important social role of allogrooming in a platyrrhine primate. *Animal Behaviour, 54*(1), 199-211.

Dubuc, C., Allen, W. L., Maestripieri, D., & Higham, J. P. (2014). Is male rhesus macaque red color ornamentation attractive to females? *Behavioral Ecology and Sociobiology*, *68*(7), 1215-1224.

Dubuc, C., Brent, L. J., Accamando, A. K., Gerald, M. S., MacLarnon, A., Semple, S., ... Engelhardt, A. (2009). Sexual skin color contains information about the timing of the fertile phase in free-ranging *Macaca mulatta*. *International Journal of Primatology*, *30*(6), 777-789.

Dufour, V., Pascalis, O., & Petit, O. (2006). Face processing limitation to own species in primates: a comparative study in brown capuchins, Tonkean macaques and humans. *Behavioural Processes*, *73*(1), 107-113.

Dufour, V., Sueur, C., Whiten, A., & Buchanan-Smith, H. M. (2011). The impact of moving to a novel environment on social networks, activity and wellbeing in two new world primates. *American Journal of Primatology*, *73*(8), 802-811.

Dunbar, R. I. M. (2013). Primates and their societies. In R. I. M. Dunbar (Ed.), *Primate social systems,* (pp. 1-14). Bristol, England: Springer Science & Business Media.

Digman, J. M. (1990). Personality structure: Emergence of the five-factor model. *Annual Review of Psychology, 41*(1), 417-440.

Donaldson, Z. R., Kondrashov, F. A., Putnam, A., Bai, Y., Stoinski, T. L., Hammock, E. A., & Young, L. J. (2008). Evolution of a behavior-linked microsatellite-containing element in the 5' flanking region of the primate AVPR1A gene. *BMC Evolutionary Biology, 8*(180). doi: 10.1186/1471-2148-8-180

Donnellan, M. B., & Lucas, R. E. (2008). Age differences in the Big Five across the life span: evidence from two national samples. *Psychology and Aging, 23*(3), 558-566. doi: 10.1037/a0012897

Drayton, L. A., & Santos, L. R. (2016). A decade of theory of mind research on Cayo Santiago: Insights into rhesus macaque social cognition. *American Journal of Primatology, 78*(1), 106-116. doi: 10.1002/ajp.22362

Eaton, G. G., Kelley, S. T., Axthelm, M. K., Iliff-Sizemore, S. A., & Shiigi, S. M. (1994). Psychological well-being in paired adult female rhesus (*Macaca mulatta*). *American Journal of Primatology*, *33*(2), 89-99.

Ebstein, R. P., Israel, S., Lerer, E., Uzefovsky, F., Shalev, I., Gritsenko, I., . . . Yirmiya, N. (2009). Arginine vasopressin and oxytocin modulate human social behavior. *Annals of the New York Academcy of Sciences, 1167*, 87-102. doi: 10.1111/j.1749-6632.2009.04541.x

Eckardt, W., Steklis, H. D., Steklis, N. G., Fletcher, A. W., Stoinski, T. S., & Weiss, A. (2015). Personality dimensions and their behavioral correlates in wild Virunga mountain gorillas (*Gorilla beringei beringei*). *Journal of Comparative Psychology, 129*(1), 26-41. doi: 10.1037/a0038370

Edgar, J. L., Nicol, C. J., Clark, C. C. A., & Paul, E. S. (2012). Measuring empathic responses in animals. *Applied Animal Behaviour Science, 138*(3-4), 182-193. doi: 10.1016/j.applanim.2012.02.006

Edgar, J. L., Nicol, C. J., Pugh, C. A., & Paul, E. S. (2013). Surface temperature changes in response to handling in domestic chickens. *Physiology & behavior*, *119*, 195-200.

Edwards, S. D., & Snowdon, C. T. (1980). Social behavior of captive, group-living orang-utans. *International Journal of Primatology, 1*(1), 39-62.

Eibl-Eibesfeldt, I. (1961). The fighting behavior of animals. *Scientific American, 205*(6), 112-122.

Ekman, P., & Friesen, W. (1971). Constants across cultures in the face and emotion. *Journal of Personality and Social Psychology, 17*(2), 124-129.

Ekman, P., & Friesen, W. V. (1978). *Manual for the facial action coding system. Consulting Psychologists Press*.

Emerson, E., Kiernan, C., Alborz, A., Reeves, D., Mason, H., Swarbrick, R., ... Hatton, C. (2001). The prevalence of challenging behaviors: A total population study. *Research in developmental disabilities*, *22*(1), 77-93.

Emery, N. J. (2000). The eyes have it: the neuroethology, function and evolution of social gaze. *Neuroscience and Biobehavioral Reviews, 24*, 581-604.

Engh, A. L., Hoffmeier, R. R., Cheney, D. L., & Seyfarth, R. M. (2006). Who, me? Can baboons infer the target of vocalizations? *Animal Behaviour, 71*(2), 381-387. doi: 10.1016/j.anbehav.2005.05.009

Enomoto, T. (1990). Social play and sexual behavior of the bonobo (*Pan paniscus*) with special reference to flexibility. *Primates*, *31*(4), 469-480.

Erdheim, J., Wang, M., & Zickar, M. J. (2006). Linking the Big Five personality constructs to organizational commitment. *Personality and Individual Differences, 41*(5), 959-970. doi: 10.1016/j.paid.2006.04.005

Eysenck, H. J. (1977). Personality and factor analysis: A reply to Guilford. *Psychological Bulletin, 84*(3), 405-411.

Fagot, J., Thompson, R. K., & Parron, C. (2010). How to read a picture: Lessons from nonhuman primates. *Proceedings of the National Academy of Sciences*, *107*(2), 519-520.

Farroni, T., Johnson, M. H., & Csibra, G. (2004). Mechanisms of eye gaze perception during infancy. *Journal of Cognitive Neuroscience, 16*(8), 1320-1326.

Feinberg, A. P., & Fallin, M. D. (2015). Epigenetics at the crossroads of genes and the environment. *Jama*, *314*(11), 1129-1130.

Feinberg, D. R., Jones, B. C., DeBruine, L. M., Moore, F. R., Smith, M. J. L., Cornwell, R. E., ... Perrett, D. I. (2005). The voice and face of woman:

One ornament that signals quality? *Evolution and Human Behavior*, *26*(5), 398-408.

Ferdowsian, H. R., Durham, D. L., Kimwele, C., Kranendonk, G., Otali, E., Akugizibwe, T., ... & Johnson, C. M. (2011). Signs of mood and anxiety disorders in chimpanzees. *PLoS One*, *6*(6), e19855

Ferrari, P. F., Gallese, V., Rizzolatti, G., & Fogassi, L. (2003). Mirror neurons responding to the observation of ingestive and communicative mouth actions in the monkey ventral premotor cortex. *European Journal of Neuroscience, 17*(8), 1703-1714. doi: 10.1046/j.1460-9568.2003.02601.x

Ferris, C. F., Albers, H. E., Wesolowski, S. M., Goldman, B. D., & Luman, S. E. (1984). Vasopressin injected into the hypothalamus triggers a stereotypic behavior in golden hamsters. *Science, 224*, 521-523.

Ferris, C. F., Lu, S. F., Messenger, T., Guillon, C. D., Heindel, N., Miller, M., . . . Simon, N. G. (2006). Orally active vasopressin V1a receptor antagonist, SRX251, selectively blocks aggressive behavior. *Pharmacology, Biochemistry, and Behavior, 83*(2), 169-174. doi: 10.1016/j.pbb.2006.01.001

Flack, J. C., de Waal, F. B., & Krakauer, D. C. (2005). Social structure, robustness, and policing cost in a cognitively sophisticated species. *The American Naturalist*, *165*(5), E126-E139.

Flack, J. C., Girvan, M., de Waal, F. B., & Krakauer, D. C. (2006). Policing stabilizes construction of social niches in primates. *Nature*, *439*(7075), 426-429.

Fleagle, J. G., Mittermeier, R. A., & Skopec, A. L. (1981). Differential habitat use by *Cebus apella* and *Saimiri sciureus* in Central Surinam. *Primates, 22*(3), 361-367.

Fragaszy, D. M., Visalberghi, E., & Fedigan, L. M. (2004). *The complete capuchin: the biology of the genus Cebus*. Cambridge, UK: Cambridge University Press.

Frank, C. K., Baron-Cohen, S., & Ganzel, B. L. (2015). Sex differences in the neural basis of false-belief and pragmatic language comprehension. *NeuroImage*, *105*, 300-311.

Franks, B., Reiss, D., Cole, P., Friedrich, V., Thompson, N., & Higgins, E. T. (2013). Predicting how individuals approach enrichment: regulatory focus in cotton-top tamarins (*Sanguinus oedipus*). *Zoo Biology, 32*(4), 427-435. doi: 10.1002/zoo.21075

Fraser, O. N., Stahl, D., & Aureli, F. (2008). Stress reduction through consolation in chimpanzees. *Proceedings of the National Academy of Sciences*, *105*(25), 8557-8562.

Freeman, H. D. (2010). *Scale development and construct validation of a chimpanzee rating scale (*Doctoral dissertation, University of Texas). Retrieved from http://repositories.lib.utexas.edu/

Freeman, H. D., & Gosling, S. D. (2010). Personality in nonhuman primates: a review and evaluation of past research. *American Journal of Primatology, 72*(8), 653-671.

Funder, D. C., Kolar, D. C., & Blackman, M. C. (1995). Agreement among judges of personality: interpersonal relations, similarity, and acquaintanceship. *Journal of Personality and Social Psychology, 69*(4), 656-672.

Galdikas, B. M. (1985). Subadult male orangutan sociality and reproductive behavior at Tanjung Puting. *American Journal of Primatology, 8*(2), 87-99.

Galdikas, B. M. F. (1995). Social and reproductive behaviour of wild adolescent female orang-utans. In R. D. Nadler, B. M. F. Galdikas, L. K. Sheeran & N. Rosen (Eds.), *The Neglected Ape,* (pp. 163-182). New York, NY: Plenum Press.

Gans, C., & Northcutt, R. G. (1983). Neural crest and the origin of vertebrates: A new head. *Science, 220*(4594), 268-273.

Gartner, M. C. (2015). Pet personality: A review. *Personality and Individual Differences, 75*, 102-113.

Gartner, M. C., & Powell, D. (2012). Personality assessment in snow leopards (*Uncia uncia*). *Zoo Biology, 31*(2), 151-165. doi: 10.1002/zoo.20385

Gartner, M. C., Powell, D. M., & Weiss, A. (2016). Comparison of subjective well being and personality assessments in the clouded leopard (*Neofelis nebulosa*), snow leopard (*Panthera uncia*), and African lion (*Panthera leo*). *Journal of Applied Animal Welfare Science*, 1-9.

Gartner, M. C., & Weiss, A. (2013). Scottish wildcat (*Felis silvestris grampia*) personality and subjective well-being: Implications for captive management. *Applied Animal Behaviour Science, 147*(3-4), 261-267. doi: 10.1016/j.applanim.2012.11.002

Geniole, S. N., Keyes, A. E., Carré, J. M., & McCormick, C. M. (2014). Fearless dominance mediates the relationship between the facial width-to-height ratio and willingness to cheat. *Personality and Individual Differences*, *57*, 59-64.

Genty, E., Breuer, T., Hobaiter, C., & Byrne, R. W. (2009). Gestural communication of the gorilla (*Gorilla gorilla*): repertoire, intentionality and possible origins. *Animal Cognition, 12*(3), 527-546. doi: 10.1007/s10071-009-0213-4

Gibson, K. R. (2002). Evolution of human intelligence: The roles of brain size and mental construction. *Brain, Behavior and Evolution, 59*, 10-20.

Goetz, S. M., Shattuck, K. S., Miller, R. M., Campbell, J. A., Lozoya, E., Weisfeld, G. E., & Carré, J. M. (2013). Social status moderates the relationship between facial structure and aggression. *Psychological science*, 0956797613493294.

Gold, K. C., & Maple, T. L. (1994). Personality assessment in the gorilla and its utility as a management tool. *Zoo Biology*, *13*(5), 509-522.

Goldberg, L. R. (1990). An alternative 'Description of Personality: The Big-Five Factor structure. *Personality Processes and Individual Differences, 59*(6), 1216-1229.

Goldman, S., Wang, C., Salgado, M. W., Greene, P. E., Kim, M., & Rapin, I. (2009). Motor stereotypies in children with autism and other developmental disorders. *Developmental Medicine & Child Neurology*, *51*(1), 30-38.

Gomez, J. C. (1998). Do concepts of intersubjectivity apply to non-human primates? In S. Bråten (Ed.), *Intersubjective communication and emotion in early ontogeny,* (pp. 245-259). Cambridge, UK: Cambridge University Press.

Goodall, J. (2000). *In the Shadow of Man*. New York, NY: Mariner Books.

Gosling, S. D. (2001). From mice to men: What can we learn about personality from animal research? *Psychological Bulletin, 127*(1), 45-86.

Gosling, S. D., & Graybeal, A. (2007). Tree thinking: a new paradigm for integrating comparative data in psychology. *The Journal of General Psychology, 134*(2), 259-277. doi: 10.3200/GENP.134.2.259-278

Gosling, S. D., Ko, S. J., Mannarelli, T., & Morris, M. E. (2002). A room with a cue: personality judgments based on offices and bedrooms. *Journal of Personality and Social Psychology*, *82*(3), 379.

Gosling, S. D., & Vazire, S. (2002). Are we barking up the right tree? Evaluating a comparative approach to personality. *Journal of Research in Personality, 36*, 607-614.

Gothard, K. M., Brooks, K. N., & Peterson, M. A. (2009). Multiple perceptual strategies used by macaque monkeys for face recognition. *Animal cognition*, *12*(1), 155-167.

Graham, J. (1961). Lavater's physiognomy in England. *Journal of the History of Ideas*, *22*(4), 561-572.

Grandin, T., & Johnson, C. (2005). *Animals in Translation*. London, UK: Bloomsbury Publishing Plc.

Griffey, J. A. F. (2011). *Human and Non-Human Primate Preferences for Faces and Facial Attractiveness* (Doctoral dissertation, University of Stirling). Retrieved from https://dspace.stir.ac.uk

Gross, A. N., Engel, A. K., Richter, S. H., Garner, J. P., & Wurbel, H. (2011). Cage-induced stereotypies in female ICR CD-1 mice do not correlate with recurrent perseveration. *Behavioural Brain Research, 216*(2), 613-620. doi: 10.1016/j.bbr.2010.09.003

Guastella, A. J., Kenyon, A. R., Alvares, G. A., Carson, D. S., & Hickie, I. B. (2010). Intranasal arginine vasopressin enhances the encoding of happy and angry faces in humans. *Biological Psychiatry, 67*(12), 1220-1222. doi: 10.1016/j.biopsych.2010.03.014

Hammock, E. A. D., & Young, L. J. (2005). Microsatellite instability generates diversity in brain and sociobehavioral traits. *Science, 308*, 1630-1634.

Harada, M. L., Schneider, H., Schneider, M. C., Sampaio, I., Czelusniak, J., & Goodman, M. (1995). DNA evidence on the phylogenetic systematics of New World monkeys: support for the sister-grouping of *Cebus* and *Saimiri* from two unlinked nuclear genes. *Molecular Phylogenetics and Evolution*, *4*(3), 331-349.

Harcourt, A. H., & Stewart, K. J. (1996). Function and Meaning of Wild Gorilla 'Close' Calls 2. Correlations with Rank and Relatedness. *Behaviour, 133*(11/12), 827-845.

Hare, B., Wobber, V., & Wrangham, R. (2012). The self-domestication hypothesis: evolution of bonobo psychology is due to selection against aggression. *Animal Behaviour, 83*(3), 573-585. doi: 10.1016/j.anbehav.2011.12.007

Harlow, H. F. (1958). The Nature of Love. *American Psychologist, 13*, 673-685.

Haselhuhn, M. P., Ormiston, M. E., & Wong, E. M. (2015). Men's facial width-to-height ratio predicts aggression: a meta-analysis. [Meta-Analysis]. *PLoS ONE, 10*(4), e0122637. doi: 10.1371/journal.pone.0122637

Haselhuhn, M. P., & Wong, E. M. (2011). Bad to the bone: facial structure predicts unethical behaviour. *Proceedings of the Royal Society of London B: Biological Sciences*, rspb20111193.

Hatfield, E., Cacioppo, J. T., & Rapson, R. L. (1994). *Emotional Contagion*. USA: Cambridge University Press

Hayes, N., & Joseph, S. (2003). Big 5 correlates of three measures of subjective well-being. *Personality and Individual Differences, 34*, 723–727.

Henderson, A. J., Holzleitner, I. J., Talamas, S. N., & Perrett, D. I. (2016). Perception of health from facial cues. *Philosophical Transactions of the Royal Society B*, *371*(1693), 20150380.

Herrelko, E. S. (2011). *An assessment of the development of a cognitive research programme and introductions in zoo-housed chimpanzees* (Doctoral dissertation, University of Stirling). Retrieved from https://dspace.stir.ac.uk

Herrelko, E. S., Vick, S. J., & Buchanan-Smith, H. M. (2012). Cognitive research in zoo-housed chimpanzees: influence of personality and impact on welfare. *American Journal of Primatology, 74*(9), 828-840. doi: 10.1002/ajp.22036

Herrmann, E., & Call, J. (2012). Are there geniuses among the apes? *Philosophical Transactions of the Royal Society B: Biological Sciences, 367*(1603), 2753-2761. doi: 10.1098/rstb.2012.0191

Herrmann, E., Call, J., Hernandez-Lloreda, M. V., Hare, B., & Tomasello, M. (2007). Humans have evolved specialized skills of social cognition: the cultural intelligence hypothesis. *Science, 317*(5843), 1360-1366. doi: 10.1126/science.1146282

Herrmann, E., Hernandez-Lloreda, M. V., Call, J., Hare, B., & Tomasello, M. (2009). The structure of individual differences in the cognitive abilites of children and chimpanzees. *Psychological Science*, 1-9.

Hill, S. P., & Broom, D. M. (2009). Measuring zoo animal welfare: theory and practice. *Zoo Biology*, *28*(6), 531-544.

Hirata, S. (2009). Chimpanzee social intelligence: selfishness, altruism, and the mother-infant bond. [Review]. *Primates, 50*(1), 3-11. doi: 10.1007/s10329-008-0122-1

Hodges-Simeon, C. R., Sobraske, K. N. H., Samore, T., Gurven, M., & Gaulin, S. J. (2016). Facial Width-To-Height Ratio (fWHR) is not associated with adolescent testosterone levels. *PloS ONE*, *11*(4), e0153083.

Hoff, M. P., Nadler, R. D., Hoff, K. T., & Maple, T. L. (1994). Separation and depression in infant gorillas. *Developmental Psychobiology, 27*(7), 439-452.

Holliday, R. (2006). Epigenetics: a historical overview. *Epigenetics*, *1*(2), 76-80.

Hopkins, W. D., Donaldson, Z. R., & Young, L. J. (2012). A polymorphic indel containing the RS3 microsatellite in the 5' flanking region of the vasopressin V1a receptor gene is associated with chimpanzee (*Pan troglodytes*) personality. *Genes, Brain and Behavior, 11*(5), 552-558. doi: 10.1111/j.1601-183X.2012.00799.x

Hopkins, W. D., Keebaugh, A. C., Reamer, L. A., Schaeffer, J., Schapiro, S. J., & Young, L. J. (2014). Genetic influences on receptive joint attention in chimpanzees (*Pan troglodytes*). *Scientific Reports, 4*, 3774. doi: 10.1038/srep03774

Hopkins, W. D., Russell, J. L., & Schaeffer, J. (2014). Chimpanzee intelligence is heritable. *Current Biology*, *24*(14), 1649-1652.

Hopper, L. M., Lambeth, S. P., & Schapiro, S. J. (2012). An evaluation of the efficacy of video displays for use with chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, *74*(5), 442-449.

Husak, J. F., Kristopher Lappin, A., Fox, S. F., & Lemos-Espinal, J. A. (2006). Bite-force performance predicts dominance in male venerable collared lizards (*Crotaphytus antiquus*). *Copeia*, *2006*(2), 301-306.

Inoue-Murayama, M. (2009). Genetic polymorphism as a background of animal behavior. *Animal Science Journal, 80*(2), 113-120. doi: 10.1111/j.1740-0929.2008.00623.x

IUCN (2015). The IUCN Red List of Threatened Species. Version 2015-4, from http://www.iucnredlist.org

Iwanicki, S., & Lehmann, J. (2015). Behavioral and trait rating assessments of personality in common marmosets (*Callithrix jacchus*). *Journal of Comparative Psychology, 129*(3), 205-217. doi: 10.1037/a0039318

Izawa, K. (1980). Social behavior of the wild black-capped capuchin (*Cebus apella*). *Primates, 21*(4), 443-467.

Jacobs, G. H. (1993). The distribution and nature of colour vision among the mammals. *Biological Reviews*, *68*(3), 413-471.

Janson, C. H. (1990). Social correlates of individual spatial choice in foraging groups of brown capuchin monkeys, *Cebus apella*. *Animal Behaviour*, *40*(5), 910-921.

Janson, C., Baldovino, M. C., & Di Bitetti, M. (2012). The group life cycle and demography of brown capuchin monkeys (*Cebus [apella] nigritus*) in Iguazú National Park, Argentina. In P. M. Kappeler & D. P. Watts (Eds.), *Long-term field studies of primates,* (pp. 185-212). Heidelberg, Germany: Springer Science & Business Media.

John, O. P., Naumann, L. P., & Soto, C. J. (2008). Paradigm shift to the integrative Big Five trait taxonomy. In O. P. John, R. W. Robins & L. A. Pervin (Eds.), *Handbook of Personality, Third Edition: Theory and Research,* (pp. 114-158). New York, NY: The Guilford Press.

Johnson, W., & Krueger, R. F. (2004). Genetic and environmental structure of adjectives describing the domains of the Big Five Model of personality: A nationwide US twin study. *Journal of Research in Personality, 38*(5), 448-472.

Jones, K. E., Ruff, C. B., & Goswami, A. (2013). Morphology and biomechanics of the pinniped jaw: mandibular evolution without mastication. *The Anatomical Record*, *296*(7), 1049-1063.

Jolliffe, D., & Farrington, D. P. (2006). Development and validation of the Basic Empathy Scale. *Journal of Adolescence*, *29*(4), 589-611.

Judge, P. G., & de Waal, F. B. (1993). Conflict avoidance among rhesus monkeys: coping with short-term crowding. *Animal Behaviour, 46*(2), 221-232.

Kalcher, E., Franz, C., Crailsheim, K., & Preuschoft, S. (2008). Differential onset of infantile deprivation produces distinctive long-term effects in adult ex-laboratory chimpanzees (*Pan troglodytes*). *Developmental Psychobiology, 50*(8), 777-788. doi: 10.1002/dev.20330

Kalcher-Sommersguter, E., Franz-Schaider, C., Preuschoft, S., & Crailsheim, K. (2013). Long-term evaluation of abnormal behavior in adult ex-laboratory chimpanzees (*Pan troglodytes*) following re-socialization. *Behavioral Sciences*, *3*(1), 99-119.

Kano, F., Hirata, S., Deschner, T., Behringer, V., & Call, J. (2016). Nasal temperature drop in response to a playback of conspecific fights in chimpanzees: A thermo-imaging study. *Physiology & Behavior*, *155*, 83-94.

Kano, F., Tanaka, M., & Tomonaga, M. (2008). Enhanced recognition of emotional stimuli in the chimpanzee (*Pan troglodytes*). *Animal Cognition*, *11*(3), 517-524.

Kano, F., & Tomonaga, M. (2009). How chimpanzees look at pictures: a comparative eye-tracking study. *Proceedings of the Royal Society of London B: Biological Sciences*, doi: 10.1098/rspb-2008.

Kano, F., & Tomonaga, M. (2010). Attention to emotional scenes including whole-body expressions in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *124*(3), 287.

Kanske, P., Böckler, A., Trautwein, F. M., & Singer, T. (2015). Dissecting the social brain: Introducing the EmpaToM to reveal distinct neural networks and brain–behavior relations for empathy and Theory of Mind. *Neuroimage*, *122*, 6-19.

Kappeler, P. M., & van Schaik, C. P. (2002). Evolution of primate social systems. *International Journal of Primatology, 23*(4), 707-740.

Kawai, N., & Matsuzawa, T. (2000). Cognition: numerical memory span in a chimpanzee. *Nature*, *403*(6765), 39-40.

Kim, S. (2012). Audience involvement and film tourism experiences: Emotional places, emotional experiences. *Tourism Management*, *33*(2), 387-396.

King, J. E., & Figueredo, A. J. (1997). The Five-Factor Model plus dominance in chimpanzee personality. *Journal of Research in Personality, 31*, 257-271.

King, J. E., & Landau, V. I. (2003). Can chimpanzee (*Pan troglodytes*) happiness be estimated by human raters? *Journal of Research in Personality, 37*, 1-15.

King, J. E., & Weiss, A. (2011). Personality from the perspective of a primatologist. In A. Weiss, J. E. King & L. Murray (Eds.), *Personality and Temperament in Nonhuman Primates,* (pp. 77-99). London, UK: Springer Science & Business Media.

King, J. E., Weiss, A., & Farmer, K. H. (2005). A chimpanzee (*Pan troglodytes*) analogue of cross-national generalization of personality structure: zoological parks and an African sanctuary. *Journal of Personality*, *73*(2), 389-410.

King, J. E., Weiss, A., & Sisco, M. M. (2008). Aping humans: age and sex effects in chimpanzee (*Pan troglodytes*) and human (*Homo sapiens*) personality. *Journal of Comparative Psychology, 122*(4), 418-427. doi: 10.1037/a0013125

Knafo, A., Israel, S., Darvasi, A., Bachner-Melman, R., Uzefovsky, F., Cohen, L., . . . Ebstein, R. P. (2008). Individual differences in allocation of funds in the dictator game associated with length of the arginine vasopressin 1a receptor RS3 promoter region and correlation between RS3 length and hippocampal mRNA. *Genes, Brain and Behavior, 7*(3), 266-275. doi: 10.1111/j.1601-183X.2007.00341.x

Knafo-Noam, A., Uzefovsky, F., Israel, S., Davidov, M., & Zahn-Waxler, C. (2015). The prosocial personality and its facets: genetic and environmental architecture of mother-reported behavior of 7-year-old twins. *Frontiers in psychology*, *6*, 112.

Konečná, M., Lhota, S., Weiss, A., Urbanek, T., Adamova, T., & Pluhacek, J. (2008). Personality in free-ranging Hanuman langur (*Semnopithecus entellus*) males: subjective ratings and recorded behavior. *Journal of Comparative Psychology, 122*(4), 379-389. doi: 10.1037/a0012625

Konečná, M., Weiss, A., Lhota, S., & Wallner, B. (2012). Personality in barbary macaques (*Macaca sylvanus*): Temporal stability and social rank. *Journal of Research in Personality, 46*(5), 581-590. doi: 10.1016/j.jrp.2012.06.004

Koski, S. E., & Burkart, J. M. (2015). Common marmosets show social plasticity and group-level similarity in personality. *Scientific Reports, 5*, 8878. doi: 10.1038/srep08878

Koski, S. E., & Sterck, E. H. M. (2007). Triadic postconflict affiliation in captive chimpanzees: does consolation console? *Animal Behaviour, 73*(1), 133-142. doi: 10.1016/j.anbehav.2006.04.009

Kramer, R. S. (2015). Facial width-to-height ratio in a large sample of commonwealth games athletes. *Evolutionary Psychology*, *13*(1), doi: 10.1177/147470491501300112

Kramer, R. S., King, J. E., & Ward, R. (2011). Identifying personality from the static, nonexpressive face in humans and chimpanzees: evidence of a shared system for signaling personality. *Evolution and Human Behavior*, *32*(3), 179-185.

Kramer, R. S., & Ward, R. (2010). Internal facial features are signals of personality and health. *The Quarterly Journal of Experimental Psychology*, *63*(11), 2273-2287.

Kramer, R. S., & Ward, R. (2012). Cues to personality and health in the facial appearance of chimpanzees (*Pan troglodytes*). *Evolutionary Psychology*, *10*(2), 147470491201000210.

Kranendonk, G., & Schippers, E. P. (2014). A pilot study on the effects of a change in behavioural management on the behaviour of captive chimpanzees (*Pan troglodytes*). *Applied Animal Behaviour Science*, *160*, 127-137.

Krebs, J. R., & Dawkins, R. (1984). Animal signals: mind-reading and manipulation. In J.R. Krebs and N.B. Davies (Eds.) *Behavioural ecology: an evolutionary approach, 2nd edition*, (pp. 380-402). Oxford, UK: Blackwell Scientific Publications.

Kret, M. E., Jaasma, L., Bionda, T., & Wijnen, J. G. (2016). Bonobos (*Pan paniscus*) show an attentional bias toward conspecifics' emotions. *Proceedings of the National Academy of Sciences*, *113*(14), 3761-3766.

Kroslak, T., Laforge, K. S., Gianotti, R. J., Ho, A., Nielsen, D. A., & Kreek, M. J. (2007). The single nucleotide polymorphism A118G alters functional properties of the human mu opioid receptor. *Journal of Neurochemistry, 103*(1), 77-87. doi: 10.1111/j.1471-4159.2007.04738.x

Künzl, C., & Sachser, N. (1999). The behavioral endocrinology of domestication: a comparison between the domestic guinea pig (*Cavia aperea* f. *porcellus*) and its wild ancestor, the cavy (*Cavia aperea*). *Hormones and Behavior, 35*, 28-37.

Kuraoka, K., & Nakamura, K. (2011). The use of nasal skin temperature measurements in studying emotion in macaque monkeys. *Physiology & behavior*, *102*(3), 347-355.

Kwan, V. S. Y., Gosling, S. D., & John, O. P. (2008). Anthropomorphism as a special case of social percpetion: a cross-species social relations model analysis of humans and dogs. *Social Cognition, 26*(2), 129-142.

Lacreuse, A., Schatz, K., Strazzullo, S., King, H. M., & Ready, R. (2013). Attentional biases and memory for emotional stimuli in men and male rhesus monkeys. *Animal cognition*, *16*(6), 861-871.

Lai, M. C., Lombardo, M. V., Pasco, G., Ruigrok, A. N., Wheelwright, S. J., Sadek, S. A., ... & Braon-Cohen, S. (2011). A behavioral comparison of male and female adults with high functioning autism spectrum conditions. *PloS ONE*, *6*(6), e20835.

Lappin, A. K., & Husak, J. F. (2005). Weapon performance, not size, determines mating success and potential reproductive output in the collared lizard (*Crotaphytus collaris*). *The American Naturalist*, *166*(3), 426-436.

Lavelli, M., & Fogel, A. (2002). Developmental changes in mother-infant face-to-face communication: birth to 3 months. *Developmental psychology, 38*(2), 288-305.

LeDoux, J. E. (2000). Emotion Circuits in the Brain. *Annual Review of Neuroscience, 23*, 155-184.

Lefevre, C. E., & Lewis, G. J. (2013). Perceiving aggression from facial structure: further evidence for a positive association with facial width-to-height ratio and masculinity, but not for moderation by self-reported dominance. *European Journal of Personality*, doi: 10.1002/per.1942

Lefevre, C. E., Lewis, G. J., Bates, T. C., Dzhelyova, M., Coetzee, V., Deary, I. J., & Perrett, D. I. (2012). No evidence for sexual dimorphism of facial width-to-height ratio in four large adult samples. *Evolution and Human Behavior*, *33*(6), 623-627.

Lefevre, C. E., Lewis, G. J., Perrett, D. I., & Penke, L. (2013). Telling facial metrics: facial width is associated with testosterone levels in men. *Evolution and Human Behavior*, *34*(4), 273-279.

Lefevre, C. E., Wilson, V. A., Morton, F. B., Brosnan, S. F., Paukner, A., & Bates, T. C. (2014). Facial width-to-height ratio relates to alpha status and assertive personality in capuchin monkeys. *PLoS ONE, 9*(4), e93369. doi: 10.1371/journal.pone.0093369

Lehmann, J., & Boesch, C. (2004). To fission or to fusion: effects of community size on wild chimpanzee (*Pan troglodytes verus*) social organisation. *Behavioral Ecology and Sociobiology*, *56*(3), 207-216.

Leonardi, R., Buchanan-Smith, H. M., Dufour, V., MacDonald, C., & Whiten, A. (2010). Living together: behavior and welfare in single and mixed species groups of capuchin (C*ebus apella*) and squirrel monkeys (*Saimiri sciureus*). *American Journal of Primatology*, *72*(1), 33-47.

Lesch, K. P., Bengel, D., Heils, A., Sabol, S. Z., Greenberg, B. D., Petri, S., . . . Murphy, D. L. (1996). Association of anxiety-related traits with a polymorphism in the serotonin transporter gene regulatory region. *Science, 274*(5292), 1527 - 1531.

Lewis, G. J., Lefevre, C. E., & Bates, T. C. (2012). Facial width-to-height ratio predicts achievement drive in US presidents. *Personality and Individual Differences, 52*(7), 855-857.

Liebal, K., Pika, S., & Tomasello, M. (2006). Gestural communication of orangutans (*Pongo pygmaeus*). *Gesture, 6*(1), 1-38.

Little, A.C., Burt, D. M., & Perrett, D. I. (2006). Assortative mating for perceived facial personality traits. *Personality and Individual Differences, 40,* 973-984.

Llorente, M., Riba, D., Ballesta, S., Feliu, O., & Rostán, C. (2015). Rehabilitation and socialization of chimpanzees (*Pan troglodytes*) used for entertainment and as pets: an 8-year study at Fundació Mona. *International Journal of Primatology*, *36*(3), 605-624.

Lorenzo-Seva, U., & Ten Berge, J. M. (2006). Tucker's congruence coefficient as a meaningful index of factor similarity. *Methodology, 2*(2), 57-64.

Ludwig, N., Gargano, M., Luzi, F., Carenzi, C., & Verga, M. (2007). Technical note: Applicability of infrared thermography as a non invasive measurements of stress in rabbit. *World Rabbit Science*, *15*(4), 199-206.

Lykken, D. & Tellegen, A. (1996). Happiness is a stochastic phenomenon. *Psychological Science, 7*(3), 186-189.

Macdonald, C., & Whiten, A. (2011). The 'Living Links to Human Evolution' Research Centre in Edinburgh Zoo: a new endeavour in collaboration. *International Zoo Yearbook*, *45*(1), 7-17.

Manson, J. H., & Perry, S. (2013). Personality structure, sex differences, and temporal change and stability in wild white-faced capuchins (*Cebus capucinus*). *Journal of comparative psychology, 127*(3), 299-311. doi: 10.1037/a0031316

Marechal, L., Genty, E., & Roeder, J. J. (2010). Recognition of faces of known individuals in two lemur species (*Eulemur fulvus* and *E. macaco*). *Animal Behaviour*, *79*(5), 1157-1163.

Marrus, N., Faughn, C., Shuman, J., Petersen, S. E., Constantino, J. N., Povinelli, D. J., & Pruett, J. R. (2011). Initial description of a quantitative, cross-species (chimpanzee–human) social responsiveness measure. *Journal of the American Academy of Child & Adolescent Psychiatry*, *50*(5), 508-518.

Mason, G. J. (1991). Stereotypies: a critical review. *Animal behaviour*, *41*(6), 1015-1037.

Mason, G., Clubb, R., Latham, N., & Vickery, S. (2007). Why and how should we use environmental enrichment to tackle stereotypic behaviour? *Applied Animal Behaviour Science*, *102*(3), 163-188.

Mason, G. J., & Latham, N. R. (2004). Can't stop, won't stop: is stereotypy a reliable animal welfare indicator? *Animal Welfare, 13,* 57-69.

Massen, J. J., & Koski, S. E. (2014). Chimps of a feather sit together: chimpanzee friendships are based on homophily in personality. *Evolution and Human Behavior*, *35*(1), 1-8.

Massen, J. J., Sterck, E. H., & De Vos, H. (2010). Close social associations in animals and humans: functions and mechanisms of friendship. *Behaviour*, *147*(11), 1379-1412.

Masten, C. L., Morelli, S. A., & Eisenberger, N. I. (2011). An fMRI investigation of empathy for 'social pain'and subsequent prosocial behavior. *Neuroimage*, *55*(1), 381-388.

Martau, P. A., Caine, N. G., & Candland, D. K. (1985). Reliability of the Emotions Profile Index, Primate Form, with *Papio hamadryas*, *Macaca fuscata*, and two *Saimiri* species. *Primates, 26*(4), 501-505.

Martin, L. J., Spicer, D. M., Lewis, M. H., Gluck, J. P. & Cork, L. C. (1991). Social deprivation of infant rhesus monkeys alters the chemoarchitecture of the brain: I. subcortical regions. *The Journal of Neuroscience, 11*(11), 3344-3358.

Marty, J. S., Higham, J. P., Gadsby, E. L., & Ross, C. (2009). Dominance, coloration, and social and sexual behavior in male drills *Mandrillus leucophaeus*. *International Journal of Primatology*, *30*(6), 807-823.

Matsuzawa, T. (1985). Colour naming and classification in a chimpanzee (*Pan troglodytes*). *Journal of Human Evolution*, *14*(3), 283-291.

Matsuzawa , T. (2006). Evolutionary origins of the human mother-infant relationship. In T. Matsuzawa, M., Tomonaga, & M. Tanaka (Eds.), *Cognitive development in chimpanzees,* (pp. 127-141). Tokyo, Japan: Springer.

Matsuzawa, T., Tomonaga, M. & Tanaka, M. (2006). *Cognitive development in chimpanzees*. Tokyo, Japan: Springer.

Maynard Smith, J. & Harper, D. (2003). *Animal signals*. Oxford University Press.

McCrae, R. R., & Costa, P. T. (1985). Updating Norman's "adequacy taxonomy": Intelligence and personality dimensions in natural language and in questionnaires. *Journal of Personality and Social Psychology, 49*(3), 710-721.

McCrae, R. R., & Costa, P. T. (1987). Validation of the Five-Factor Model of Personality Across Instruments and Observers. *Journal of Personality and Social Psychology, 52*(1), 81-90.

McCrae, R. R., & John, O. P. (1992). An Introduction to the Five-Factor Model and Its Applications. *Journal of Personality, 60*(2), 175-215.

McCrae, R. R., & Sutin, A. R. (2009). Openness to experience. In M. R. Leary & R. H. Hoyle (Eds.), *Handbook of individual differences in social behavior*, (pp. 257-273). New York, USA: Guilford Press.

McCrae, R. R., Zonderman, A. B., Costa, P. T. J., Bond, M. H., & Paunonen, S. V. (1996). Evaluating replicability of factors in the Revised NEO Personality Inventory: Confirmatory factor analysis versus Procrustes rotation. *Journal of Personality and Social Psychology, 70*(3), 552.

McGreevy, P., Warren-Smith, A., & Guisard, Y. (2012). The effect of double bridles and jaw-clamping crank nosebands on temperature of eyes and facial skin of horses. *Journal of Veterinary Behavior: Clinical Applications and Research*, *7*(3), 142-148.

McNelis, N. L., & Boatright-Horowitz, S. L. (1998). Social monitoring in a primate group: the relationship between visual attention and hierarchical ranks. *Animal Cognition*, *1*(1), 65-69.

Meder, A. (1989). Effects of hand-rearing on the behavioral development of infant and juvenile gorillas (*Gorilla g. gorilla*). *Developmental Psychobiology, 22*(4), 357-376.

Mehta, P. H., & Gosling, S. D. (2008). Bridging human and animal research: A comparative approach to studies of personality and health. *Brain, Behavior and Immunity, 22*, 651-661.

Melis, A. P., Warneken, F., Jensen, K., Schneider, A. C., Call, J., & Tomasello, M. (2010). Chimpanzees help conspecifics obtain food and non-food items. *Proceedings of the Royal Society of London B: Biological Sciences*, 1-9, doi: 10.1098/rspb20101735.

Mileva, V. R., Cowan, M. L., Cobey, K. D., Knowles, K. K., & Little, A. C. (2014). In the face of dominance: Self-perceived and other-perceived dominance are positively associated with facial-width-to-height ratio in men. *Personality and Individual Differences, 69*, 115-118. doi: 10.1016/j.paid.2014.05.019

Miller, L. C., & Nadler, R. D. (1981). Mother-Infant relations and infant development in captive chimpanzees and orang-utans. *International Journal of Primatology, 2*(3), 247-261.

Mills, S. K., & Beatty, J. H. (1979). The propensity interpretation of fitness. *Philosophy of Science, 46*, 263-286.

Mitani, J. C., McGrew, W. C., & Wrangham, R. (2006). Toshisada Nishida's contributions to primatology [Biography Historical Article]. *Primates, 47*(1), 2-5. doi: 10.1007/s10329-005-0138-8

Mitchell, C. L., Boinski, S., & van Schaik, C. P. (1991). Competitive regimes and female bonding in two species of squirrel monkeys (*Saimiri oerstedi* and *S. sciureus*). *Behavioral Ecology and Sociobiology, 28*, 55-60.

Mitchell, G. D., Raymond, E. J., Ruppenthal, G. C., & Harlow, H. F. (1966). Long-term effects of total social isolation upon behaviour of rhesus macaques. *Psychological Reports, 18*, 567-580.

Mooradian, T. A., Davis, M., & Matzler, K. (2011). Dispositional empathy and the hierarchical structure of personality. *The American Journal of Psychology*, *124*(1), 99-109.

Moore, R. C., Dev, S. I., Jeste, D. V., Dziobek, I., & Eyler, L. T. (2015). Distinct neural correlates of emotional and cognitive empathy in older adults. *Psychiatry Research: Neuroimaging*, *232*(1), 42-50.

Morgan, K. N., & Tromborg, C. T. (2007). Sources of stress in captivity. *Applied Animal Behaviour Science, 102*(3), 262-302.

Morimoto, Y., & Fujita, K. (2011). Capuchin monkeys (*Cebus apella*) modify their own behaviors according to a conspecific's emotional expressions. *Primates, 52*(3), 279-286. doi: 10.1007/s10329-011-0249-3

Morimura, N., & Matsuzawa, T. (2001). Memory of movies by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *115*(2), 152.

Morton, F. B., Lee, P. C., & Buchanan-Smith, H. M. (2013). Taking personality selection bias seriously in animal cognition research: a case study in capuchin monkeys (*Sapajus apella*). *Animal Cognition, 16*(4), 677-684. doi: 10.1007/s10071-013-0603-5

Morton, F. B., Lee, P. C., Buchanan-Smith, H. M., Brosnan, S. F., Thierry, B., Paukner, A., . . . Weiss, A. (2013). Personality structure in brown capuchin monkeys (*Sapajus apella*): Comparisons with chimpanzees (*Pan troglodytes*), orangutans (*Pongo* spp.), and rhesus macaques (*Macaca mulatta*). *Journal of Comparative Psychology, 127*(3), 282-298. doi: 10.1037/a0031723.supp

Morton, F. B., Weiss, A., Buchanan-Smith, H. M., & Lee, P. C. (2015). Capuchin monkeys with similar personalities have higher-quality relationships independent of age, sex, kinship and rank. *Animal Behaviour, 105*, 163-171. doi: 10.1016/j.anbehav.2015.04.013

Morton, F. B., Brosnan, S. F., Prétôt, L., Buchanan-Smith, H. M., O’Sullivan, E., Stocker, M., ... Wilson, V. A. (2016). Using photographs to study animal social cognition and behaviour: Do capuchins’ responses to photos reflect reality? *Behavioural Processes*, *124*, 38-46.

Muller, N. M. (2002). Agonistic relations among Kanyawara chimpanzees. In C. Boesch, G. Hohmann & L. F. Marchant (Eds.), *Behavioural diversity in* *chimpanzees and bonobos*, (pp. 112-124). Cambridge, UK: Cambridge University Press.

Munafo, M. R., Clark, T. G., Moore, L. R., Payne, E., Walton, R., & Flint, J. (2003). Genetic polymorphisms and personality in healthy adults: A systematic review and meta-analysis. *Molecular Psychiatry, 8*, 471-484.

Munafo, M. R., & Flint, J. (2011). Dissecting the genetic architecture of human personality. *Trends in Cognitive Science, 15*(9), 395-400. doi: 10.1016/j.tics.2011.07.007

Munafo, M. R., Yalcin, B., Willis-Owen, S. A., & Flint, J. (2008). Association of the dopamine D4 receptor (DRD4) gene and approach-related personality traits: meta-analysis and new data. *Biological Psychiatry, 63*(2), 197-206. doi: 10.1016/j.biopsych.2007.04.006

Murray, C. M., Eberly, L. E., & Pusey, A. E. (2006). Foraging strategies as a function of season and rank among wild female chimpanzees (*Pan troglodytes*). *Behavioral Ecology, 17*(6), 1020-1028. doi: 10.1093/beheco/arl042

Myowa-Yamakoshi, M. (2006). Development of facial information processing in nonhuman primates, In T. Matsuzawa, M., Tomonaga, & M. Tanaka (Eds.), *Cognitive development in chimpanzees,* (pp. 142-154). Tokyo, Japan: Springer.

Myowa-Yamakoshi, M., Tomonaga, M., Tanaka, M., & Matsuzawa, T. (2003). Preference for human direct gaze in infant chimpanzees (*Pan troglodytes*). *Cognition, 89*(2), 113-124. doi: 10.1016/s0010-0277(03)00071-4

Myowa-Yamakoshi, M., Yamaguchi, M. K., Tomonaga, M., Tanaka, M., & Matsuzawa, T. (2005). Development of face recognition in infant chimpanzees (Pan troglodytes). *Cognitive Development, 20*(1), 49-63. doi: 10.1016/j.cogdev.2004.12.002

Nadler, R. D., & Codner, M. A. (1983). Maternal separation and reunion of an infant orang-utan. *Primates, 24*(1), 67-76.

Nakayama, K., Goto, S., Kuraoka, K., & Nakamura, K. (2005). Decrease in nasal temperature of rhesus monkeys (*Macaca mulatta*) in negative emotional state. *Physiology & behavior*, *84*(5), 783-790.

Nettle, D. (2005). An evolutionary approach to the extraversion continuum. *Evolution and Human Behavior, 26*, 363-373.

Nettle, D. (2006). The evolution of personality variation in humans and other animals. *American Psychologist, 61*(6), 622-631.

Nishida, T., Kano, T., Goodall, J., McGrew, W. C., & Nakamura, M. (1999). Ethogram and ethnography of mahale chimpanzees. *Anthropological Science*, *107*(2), 141-188.

O'Connell, S. M. (1995). Empathy in chimpanzees: Evidence for Theory of Mind? *Primates, 36*(3), 397-410.

Okamoto, S., Tomonaga, M., Ishii, K., Kawai, N., Tanaka, M., & Matsuzawa, T. (2002). An infant chimpanzee (*Pan troglodytes*) follows human gaze. *Animal Cognition, 5*(2), 107-114. doi: 10.1007/s10071-002-0133-z

Opazo, J. C., Wildman, D. E., Prychitko, T., Johnson, R. M., & Goodman, M. (2006). Phylogenetic relationships and divergence times among New World monkeys (Platyrrhini, Primates). *Molecular Phylogenetics and Evolution, 40*(1), 274-280. doi: 10.1016/j.ympev.2005.11.015

Overman, W. H., & Doty, R. W. (1980). Prolonged visual memory in macaques and man. *Neuroscience*, *5*(11), 1825-1831.

Özener, B. (2012). Facial width-to-height ratio in a Turkish population is not sexually dimorphic and is unrelated to aggressive behavior. *Evolution and Human Behavior*, *33*(3), 169-173.

Panksepp, J. (1982). Toward a general psychobiological theory of emotions. *The Behavioural and Brain Sciences, 5*, 407-467.

Panksepp, J. (2011). The basic emotional circuits of mammalian brains: do animals have affective lives? *Neuroscience and Biobehavioral Reviews, 35*(9), 1791-1804. doi: 10.1016/j.neubiorev.2011.08.003

Pardo, C. A., & Eberhart, C. G. (2007). The neurobiology of Autism. *Brain Pathology, 17*(4), 434-447. doi: 10.1111/j.1750-3639.2007.00102.x

Parnell, R. J. (2002). *The Social Structure and Behaviour of Western Lowland Gorillas (Gorilla gorilla gorilla) at Mbeli Bai, Republic of Congo*. (Doctoral dissertation, University of Stirling). Retrieved from https://dspace.stir.ac.uk

Parr, L. A. (2001). Cognitive and physiological markers of emotional awareness in chimpanzees (*Pan troglodytes*). *Animal Cognition, 4*(3-4), 223-229. doi: 10.1007/s100710100085

Parr, L. A. (2003). The discrimination of faces and their emotional content by chimpanzees (*Pan troglodytes*). *Annals of the New York Academy of Sciences, 1000*(1), 56-78.

Parr, L. A. (2011). The evolution of face processing in primates. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *366*(1571), 1764-1777.

Parr, L. A., & Hopkins, W. D. (2000). Brain temperature asymmetries and emotional perception in chimpanzees, *Pan troglodytes*. *Physiology & behavior, 71*(3), 363-371.

Parr, L. A., Hopkins, W. D., & de Waal, F. B. (1998). The perception of facial expressions by chimpanzees, *Pan troglodytes*. *Evolution of Communication, 2*(1), 1-23.

Parr, L. A., & Waller, B. M. (2006). Understanding chimpanzee facial expression: insights into the evolution of communication. *Social Cognitive and Affective Neuroscience, 1*(3), 221-228.

Parr, L. A., Waller, B. M., & Fugate, J. (2005). Emotional communication in primates: implications for neurobiology. *Current Opinion in Neurobiology, 15*(6), 716-720. doi: 10.1016/j.conb.2005.10.017

Parr, L. A., Waller, B. M., Vick, S. J., & Bard, K. A. (2007). Classifying chimpanzee facial expressions using muscle action. *Emotion, 7*(1), 172-181. doi: 10.1037/1528-3542.7.1.172

Pascalis, O., de Schonen, S., Morton, J., Deruelle, C., & Fabre-Grenet, M. (1995). Mother's face recognition by neonates: A replication and an extension. *Infant Behavior and Development, 18*(1), 79-85.

Patterson, N., Richter, D. J., Gnerre, S., Lander, E. S., & Reich, D. (2006). Genetic evidence for complex speciation of humans and chimpanzees. *Nature*, *441*(7097), 1103-1108.

Pavot, W., & Diener, E. (1993). Review of the satisfaction with life scale. *Psychological Assessment*, *5*(2), 164-172

Pederson, A. K., King, J. E., & Landau, V. I. (2005). Chimpanzee (*Pan troglodytes*) personality predicts behavior. *Journal of Research in Personality, 39*(5), 534-549. doi: 10.1016/j.jrp.2004.07.002

Peltola, M. J., Leppänen, J. M., Palokangas, T., & Hietanen, J. K. (2008). Fearful faces modulate looking duration and attention disengagement in 7-month-old infants. *Developmental Science*, *11*(1), 60-68.

Penton-Voak, I. S., Jones, B. C., Little, A. C., Baker, S., Tiddeman, B., Burt, D. M., & Perrett, D. I. (2001). Symmetry, sexual dimorphism in facial proportions and male facial attractiveness. *Proceedings of the Royal Society of London B: Biological Sciences*, *268*(1476), 1617-1623.

Penton-Voak, I. S., Pound, N., Little, A. C., & Perrett, D. I. (2006). Personality judgments from natural and composite facial images: More evidence for a “kernel of truth” in social perception. *Social Cognition*, *24*(5), 607-640.

Perelman, P., Johnson, W. E., Roos, C., Seuanez, H. N., Horvath, J. E., Moreira, M. A., . . . Pecon-Slattery, J. (2011). A molecular phylogeny of living primates. *PLoS Genetics, 7*(3), e1001342. doi: 10.1371/journal.pgen.1001342

Perry, B. D., Pollard, R. A., Blakley, T. L., Baker, W. L., & Vigilante, D. (1995). Childhood trauma, the neurobiology of adaptation, and “use-dependent” development of the brain: How “states” become “traits”. *Infant Mental Health Journal, 16*(4), 271-291.

Pokorny, J. J., & de Waal, F. (2009a). Face recognition in capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, *123*(2), 151.

Pokorny, J. J., & de Waal, F. B. (2009b). Monkeys recognize the faces of group mates in photographs. *Proceedings of the National Academy of Sciences*, *106*(51), 21539-21543.

Polderman, T. J., Benyamin, B., De Leeuw, C. A., Sullivan, P. F., Van Bochoven, A., Visscher, P. M., & Posthuma, D. (2015). Meta-analysis of the heritability of human traits based on fifty years of twin studies. *Nature genetics*, *47*(7), 702-709.

Pollick, A. S., & De Waal, F. B. (2007). Ape gestures and language evolution. *Proceedings of the National Academy of Sciences*, *104*(19), 8184-8189.

Pound, N., Penton-Voak, I. S., & Surridge, A. K. (2009). Testosterone responses to competition in men are related to facial masculinity. *Proceedings of the Royal Society of London B: Biological Sciences*, *276*(1654), 153-159.

Premack, D., & Woodruff, G. (1978). Does the chimpanzee have a theory of mind? *Behavioral and Brain Sciences, 1*(4), 515-526.

Preuschoft, S. (1992). “Laughter” and “smile” in barbary macaques (*Macaca sylvanus*). *Ethology, 91*(3), 220-236.

Pusey, A., Williams, J., & Goodall, J. (1997). The influence of dominance rank on the reproductive success of female chimpanzees. *Science*, *277*(5327), 828-831.

R Core Team (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Reimers, M., Schwarzenberger, F., & Preuschoft, S. (2007). Rehabilitation of research chimpanzees: stress and coping after long-term isolation. *Hormones and Behavior, 51*(3), 428-435. doi: 10.1016/j.yhbeh.2006.12.011

Rentfrow, P. J., Gosling, S. D., & Potter, J. (2008). A theory of the emergence, persistence and expression of geogrpahic variation in psychological characteristics. *Perspectives on Psychological Science, 3*(5), 339-369.

Ridley, R. M., & Baker, H. F. (1982). Stereotypy in monkeys and humans. *Psychological Medicine, 12*(01), 61-72. doi: 10.1017/s0033291700043294

Rilling, J. K., DeMarco, A. C., Hackett, P. D., Thompson, R., Ditzen, B., Patel, R., & Pagnoni, G. (2012). Effects of intranasal oxytocin and vasopressin on cooperative behavior and associated brain activity in men. *Psychoneuroendocrinology, 37*(4), 447-461. doi: 10.1016/j.psyneuen.2011.07.013

Roberts, B. W., Kuncel, N. R., Shiner, R., Caspi, A., & Goldberg, L. R. (2007). The power of personality: The comparative validity of personality traits, socioeconomic status, and cognitive ability for predicting important life outcomes. *Perspectives on Psychological Science, 2*(4), 313-345. doi: 10.1111/j.1745-6916.2007.00047.x

Robinson, L., Lonsdorf, E., Morton, F. B., Brosnan, S., Paukner, A., Handel, I., . . . Weiss, A. (2016). Happiness means welfare: Ratings of welfare and Subjective Well-Being correlate highly in brown capuchins (*Sapajus apella*). *Applied Animal Behavior Science, 181*, 145-151.

Romero, T., Castellanos, M. A., & de Waal, F. B. (2010). Consolation as possible expression of sympathetic concern among chimpanzees. *Proceedings of the National Academy of Sciences*, *107*(27), 12110-12115.

Rothbart, M. K. (2012). Advances in temperament. In M. Zentner & R. L. Shiner (Eds.), *Handbook of Temperament,* (pp. 3-20). New York, USA: Guilford Press.

Ruppenthal, G. C., Arling, G. L., Harlow, H. F., Sackett, G. P., & Suomi, S. J. (1976). A 10-year perspective of motherless-mother monkey behavior. *Journal of Abnormal Psychology, 85*(4), 341-349.

Russell, C. L., Bard, K. A., & Adamson, L. B. (1997). Social referencing by young chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology, 111*(2), 185-193.

RZSS (1913). Royal Zoological Society of Scotland: About, from http://www.rzss.org.uk/about-rzss/

Sambasivan, R., Kuratani, S., & Tajbakhsh, S. (2011). An eye on the head: the development and evolution of craniofacial muscles. *Development, 138*, 2401-2415.

Sapolsky, R. M. (2005). The influence of social hierarchy on primate health. *Science, 308*(5722), 648-652. doi: 10.1126/science.1106477

Schaefer, S. A., & Steklis, H. D. (2014). Personality and subjective well-being in captive male western lowland gorillas living in bachelor groups. *American Journal of Primatology, 76*(9), 879-889. doi: 10.1002/ajp.22275

Schapiro, S. J., & Lambeth, S. P. (2007). Control, choice, and asessments of the value of behavioral management to nonhuman primates in captivity. *Journal of Applied Animal Welfare Science, 10*(1), 39-47.

Schel, A. M., Rawlings, B., Claidiere, N., Wilke, C., Wathan, J., Richardson, J., . . . Slocombe, K. (2013). Network analysis of social changes in a captive chimpanzee community following the successful integration of two adult groups. *American Journal of Primatology, 75*(3), 254-266. doi: 10.1002/ajp.22101

Schel, A. M., Townsend, S. W., Machanda, Z., Zuberbühler, K., & Slocombe, K. E. (2013). Chimpanzee alarm call production meets key criteria for intentionality. *PLoS ONE*, *8*(10), e76674.

Schiffer, B., Pawliczek, C., Müller, B. W., Gizewski, E. R., & Walter, H. (2013). Why don't men understand women? Altered neural networks for reading the language of male and female eyes. *PloS ONE*, *8*(4), e60278.

Schimmack, U., Oishi, S., Furr, R. M., & Funder, D. C. (2004). Personality and life satisfaction: a facet-level analysis. *Personality and Social Psychology Bulletin, 30*(8), 1062-1075. doi: 10.1177/0146167204264292

Schinka, J. A., Letsch, E. A., & Crawford, F. C. (2002). DRD4 and novelty seeking: results of meta-analyses. *American Journal of Medical Genetics, 114*(6), 643-648. doi: 10.1002/ajmg.10649

Schmelz, M., Call, J., & Tomasello, M. (2011). Chimpanzees know that others make inferences. *Proeedings of the National Academy of Sciences, 108*(7), 3077-3079. doi: 10.1073/pnas.1000469108

Schneider, H., & Sampaio, I. (2015). The systematics and evolution of New World primates - A review. *Molecular Phylogenetics and Evolution, 82 Pt B*, 348-357. doi: 10.1016/j.ympev.2013.10.017

Schulte-Ruther, M., Markowitsch, H. J., Shah, N. J., Fink, G. R., & Piefke, M. (2008). Gender differences in brain networks supporting empathy. *Neuroimage, 42*(1), 393-403. doi: 10.1016/j.neuroimage.2008.04.180

Setchell, J. M., Smith, T., Wickings, E. J., & Knapp, L. A. (2008). Social correlates of testosterone and ornamentation in male mandrills. *Hormones and Behavior*, *54*(3), 365-372.

Seyfarth, R. M., & Cheney, D. L. (2005). The structure of social knowledge in monkeys. In F. de Waal & P. Tyac (Eds.), *Animal Social complexity: Intelligence, Culture and Individualized Societies,* (pp. 207-229). Cambridge, UK: MA Howard University Press.

Seyfarth, R. M., & Cheney, D. L. (2012). The evolutionary origins of friendship. *Annual Review of Psychology*, *63*, 153-177.

Seyfarth, R. M., Cheney, D. L., & Bergman, T. J. (2005). Primate social cognition and the origins of language. *Trends in Cognitive Sciences*, *9*(6), 264-266.

Seyfarth, R. M., Silk, J. B., & Cheney, D. L. (2012). Variation in personality and fitness in wild female baboons. *Proceedings of the National Academcy of Sciences, 109*(42), 16980-16985. doi: 10.1073/pnas.1210780109

Shamay-Tsoory, S. G. (2011). The neural bases for empathy. *Neuroscientist, 17*(1), 18-24. doi: 10.1177/1073858410379268

Shamay-Tsoory, S. G., Aharon-Peretz, J., & Perry, D. (2009). Two systems for empathy: a double dissociation between emotional and cognitive empathy in inferior frontal gyrus versus ventromedial prefrontal lesions. *Brain, 132*(Pt 3), 617-627. doi: 10.1093/brain/awn279

Shipley, B. A., Weiss, A., Der, G., Taylor, M. D., & Deary, I. J. (2007). Neuroticism, Extraversion and mortality in the UK health and lifestyle survey: A 21-year propsective cohort study. *Psychosomatic Medicine, 69*(9), 923-931.

Shrout, P. E., & Fleiss, J. L. (1979). Intraclass correlations: Uses in assessing rater reliability. *Psychological Bulletin, 86*(2), 420 - 428.

Silk, J. B., Brosnan, S. F., Vonk, J., Henrich, J., Povinelli, D. J., Richardson, A. S., ... & Schapiro, S. J. (2005). Chimpanzees are indifferent to the welfare of unrelated group members. *Nature*, *437*(7063), 1357-1359.

Silk, J. B., Seyfarth, R. M., & Cheney, D. L. (1999). The structure of social relationships among female savanna baboons in Moremi Reserve, Botswana. *Behaviour, 136*(6), 679-703.

Silverman, J. L., Yang, M., Lord, C., & Crawley, J. N. (2010). Behavioural phenotyping assays for mouse models of autism. *Nature Reviews Neuroscience, 11*(7), 490-502. doi: 10.1038/nrn2851

Simner, M. L. (1971). Newborn's response to the cry of another infant. *Developmental Psychology, 5*(1), 136-150.

Slocombe, K. E., & Zuberbühler, K. (2005). Agonistic screams in wild chimpanzees (*Pan troglodytes schweinfurthii*) vary as a function of social role. *Journal of Comparative Psychology*, *119*(1), 67.

Slocombe, K., & Zuberbühler, K. (2010). Vocal communication in chimpanzees. In E. V. Lonsdorf, S. R. Ross & T. Matsuzawa (Eds.), *The Mind of the Chimpanzee: Ecological and Experimental Perspectives*, (pp. 192-207). Chicago, IL: University of Chicago Press.

Smuts, B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W., & Struhsaker, T. T. (1987). *Primate Societies*. Chicago, IL: University of Chicago Press.

Sober, E. (2000). The Two Faces of Fitness. In R. Singh, C. Krimbas, D. Paul & J. Beatty (Eds.), *Thinking about Evolution: Historical, Philosophical, and Political Perspectives*, (pp. 309-321). Cambridge, UK: Cambridge University Press.

Sood, S., & Rogers, E. M. (2000). Dimensions of parasocial interaction by letter-writers to a popular entertainment-education soap opera in India. *Journal of Broadcasting & Electronic Media*, *44*(3), 386-414.

Soto, C. J., John, O. P., Gosling, S. D., & Potter, J. (2011a). Age differences in personality traits from 10 to 65: Big Five domains and facets in a large cross-sectional sample. *Journal of Personality and Social Psychology, 100*(2), 330-348. doi: 10.1037/a0021717

Soto, C. J., John, O. P., Gosling, S. D., & Potter, J. (2011b). Age differences in personality traits from 10 to 65: Big Five domains and facets in a large cross-sectional sample. *Journal of Personality and Social Psychology, 100*(2), 330-348. doi: 10.1037/a0021717

Southgate, V., & Hamilton, A. F. (2008). Unbroken mirrors: challenging a theory of Autism. *Trends in Cognitive Science, 12*(6), 225-229. doi: 10.1016/j.tics.2008.03.005

Staes, N., Koski, S. E., Helsen, P., Fransen, E., Eens, M., & Stevens, J. M. (2015). Chimpanzee sociability is associated with vasopressin (Avpr1a) but not oxytocin receptor gene (OXTR) variation. *Hormones and Behavior, 75*, 84-90. doi: 10.1016/j.yhbeh.2015.08.006

Stanford, C. B., Wallis, J., Mpongo, E., & Goodall, J. (1994). Hunting decisions in wild chimpanzees. *Behaviour*, *131*(1), 1-18.

Steel, P., Schmidt, J., & Shultz, J. (2008). Refining the relationship between personality and subjective well-being. *Psychological Bulletin, 134*(1), 138.

Steiper, M. E., & Young, N. M. (2006). Primate molecular divergence dates. *Molecular Phylogenetics and Evolution, 41*(2), 384-394. doi: 10.1016/j.ympev.2006.05.021

Stephen, I. D., Coetzee, V., Smith, M. L., & Perrett, D. I. (2009). Skin blood perfusion and oxygenation colour affect perceived human health. *PLoS ONE*, *4*(4), e5083.

Stevenson-Hinde, J., & Zunz, M. (1978). Subjective assessment of individual rhesus monkeys. *Primates, 19*(3), 473-482.

Stirrat, M., & Perrett, D. I. (2010). Valid facial cues to cooperation and trust: male facial width and trustworthiness. *Psychol Sci, 21*(3), 349-354. doi: 10.1177/0956797610362647

Stokes, E. J., Parnell, R. J., & Olejniczak, C. (2003). Female dispersal and reproductive success in wild western lowland gorillas (*Gorilla gorilla gorilla*). *Behavioral Ecology and Sociobiology, 54*(4), 329-339. doi: 10.1007/s00265-003-0630-3

Striedter, G. F., Avise, J. C., & Ayala, F. J. (2013). *In the Light of Evolution. Volume VI: Brain and Behavior*. Washington, D. C.: The National Academies Press.

Sulpizio, V., Committeri, G., Metta, E., Lambrey, S., Berthoz, A., & Galati, G. (2015). Visuospatial transformations and personality: evidence of a relationship between visuospatial perspective taking and self-reported emotional empathy. *Experimental Brain Research*, *233*(7), 2091-2102.

Suomi, S. J. (2006). Risk, resilience, and gene× environment interactions in rhesus monkeys. *Annals of the New York Academy of Sciences*, *1094*(1), 52-62.

Suomi, S. J., & Harlow, H. F. (1972). Depressive behavior in young monkeys subjected to vertical chamber confinement. *Journal of Comparative and Physiological Psychology, 180*(1), 11-18.

Sussman, R. W., & Garber, P. A. (2011). Cooperation, collective action, and competition in primate social interactions. In C. J. Campbell, A. Fuentes, K. C. Mackinnon, S. K. Bearder & R. S. M. Stumpf (Eds.), *Primates in Perspective: 2nd Edition,* (pp. 587-599). New York, NY: Oxford University Press.

Tabor, H. K., Risch, N. J., & Myers, R. M. (2002). Candidate-gene approaches for studying complex genetic traits: practical considerations. *Nature Reviews Genetics, 3*, 1-7.

Tanikawa, C., Zere, E., & Takada, K. (2015). Sexual dimorphism in the facial morphology of adult humans: A three-dimensional analysis. *HOMO-Journal of Comparative Human Biology, 67*(1), 23-49.

Terracciano, A., McCrae, R. R., Brant, L. J., & Costa, P. T., Jr. (2005). Hierarchical linear modeling analyses of the NEO-PI-R scales in the Baltimore Longitudinal Study of Aging. *Psychology of Aging, 20*(3), 493-506. doi: 10.1037/0882-7974.20.3.493

Thibonnier, M., Graves, M. K., Wagner, M. S., Chatelain, N., Soubrier, F., Corvol, P., . . . Jeunemaitre, X. (2000). Study of V(1)-vascular vasopressin receptor gene microsatellite polymorphisms in human essential hypertension. *Journal of Molecular and Cellular Cardiology, 32*(4), 557-564. doi: 10.1006/jmcc.2000.1108

Thornhill, R., & Gangestad, S. W. (2006). Facial sexual dimorphism, developmental stability, and susceptibility to disease in men and women. *Evolution and Human Behavior, 27*(2), 131-144. doi: 10.1016/j.evolhumbehav.2005.06.001

Tomonaga, M., Tanaka, M., Matsuzawa, T., Myowa-Yamakoshi, M., Kosugi, D., Mizuno, Y., . . . Bard, K. (2004). Development of social cognition in infant chimpanzees (*Pan troglodytes*): Face recognition, smiling, gaze, and the lack of triadic interactions. *Japanese Psychological Research, 46*(3), 227-235.

Trebicky, V., Fialova, J., Kleisner, K., Roberts, S. C., Little, A. C., & Havlicek, J. (2015). Further evidence for links between facial width-to-height ratio and fighting success: Commentary on Zilioli et al. (2014). *Aggressive Behavior, 41*(4), 331-334. doi: 10.1002/ab.21559

Trevarthen, C. (1979). Communication and cooperation in early infancy: a description of primary intersubjectivity. In M. Bullowa (Ed.), *Before Speech: the beginning of interpersonal communication*, (pp. 321-348). Cambridgem UK: Cambridge University Press. Retrieved from http://books.google.co.uk/.

Tripp, J. K. (1985). Increasing activity in captive orangutans: Provision of manipulable and edible materials. *Zoo Biology, 4*(3), 225-234.

Tronick, E. Z., Morelli, G. A., & Winn, S. (1987). Multiple caretaking of Efe (Pygmy) infants. *American Anthropologist*, *89*(1), 96-106.

Uher, J., Addessi, E., & Visalberghi, E. (2013). Contextualised behavioural measurements of personality differences obtained in behavioural tests and social observations in adult capuchin monkeys (*Cebus apella*). *Journal of Research in Personality, 47*(4), 427-444. doi: 10.1016/j.jrp.2013.01.013

Valentine, K. A., Li, N. P., Penke, L., & Perrett, D. I. (2014). Judging a man by the width of his face the role of facial ratios and dominance in mate choice at speed-dating events. *Psychological Science*, *25*(3), 806-811.

Vallone, D., Picetti, R., & Borrelli, E. (2000). Structure and function of dopamine receptors. *Neuroscience and Biobehavioral Reviews, 24*, 125-132.

Van Hooff, J. A. R. A. M. (1962). Facial expressions in higher primates. In *Symposia of the Zoological Society of London, 8,* 97-125.

Van Hooff, J. A. R. A. M. (1967). The facial displays of the catarrhine monkeys and apes. In D. Morris (Ed.), *Primate ethology,* (pp. 7-68). Aldine Publishing Company.

Van Hooff, J. A. R. A. M. (1976). The comparison of facial expressions in man and higher primates. In M. von Cranach (Ed.) *Methods of inference from animal to human behaviour,* (pp. 165-196). Aldine Publishing Company.

van Ijzendoorn, M. H., Bard, K. A., Bakermans-Kranenburg, M. J., & Ivan, K. (2009). Enhancement of attachment and cognitive development of young nursery-reared chimpanzees in responsive versus standard care. *Developmental Psychobiology, 51*(2), 173-185. doi: 10.1002/dev.20356

van Oers, K., de Jong, G., van Noordwijk, A. J., Kempenaers, B., & Drent, P. J. (2005). Contribution of genetics to the study of animal personalities: a review of case studies. *Behaviour, 142*, 1191-1212.

van Schaik, C. P. (1983). Why are diurnal primates living in groups? *Behaviour, 87*(1/2), 120-144.

van Schaik, C. P. (1999). The socioecology of fission-fusion sociality in orangutans. *Primates, 40*(1), 69-86.

Van Tol, H. H., Wu, C. M., Guan, H. C., Ohara, K., Bunzow, J. R., Civelli, O., & Jovanovic, V. (1992). Multiple dopamine D4 receptor variants in the human population. *Nature, 358*(149-152).

Vazire, S., & Gosling, S. D. (2004). e-Perceptions: personality impressions based on personal websites. *Journal of personality and social psychology*, *87*(1), 123.

Vazire, S., Gosling, S. D., Dickey, A. S., & Schapiro, S. J. (2009). Measuring personality in nonhuman animals. In R. W. Robins, R. C. Fraley & R. F. Krueger (Eds.), *Handbook of Research Methods in Personality Psychology*, (pp. 190-206). New York, NY: The Guilford Press.

Vianna, D. M., & Carrive, P. (2005). Changes in cutaneous and body temperature during and after conditioned fear to context in the rat. *European Journal of Neuroscience*, *21*(9), 2505-2512.

Vick, S. J., Waller, B. M., Parr, L. A., Pasqualini, M. C. S., & Bard, K. A. (2007). A cross-species comparison of facial morphology and movement in humans and chimpanzees using the facial action coding system (FACS). *Journal of Nonverbal Behavior, 31*(1), 1-20.

Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software, 36*(3), 1-48.

Viranyi, Z., Topal, J., Miklosi, A., & Csanyi, V. (2006). A nonverbal test of knowledge attribution: a comparative study on dogs and children. *Animal Cognition, 9*(1), 13-26. doi: 10.1007/s10071-005-0257-z

Visalberghi, E., Valenzano, D. R., & Preuschoft, S. (2006). Facial displays in *Cebus apella*. *International Journal of Primatology, 27*(6), 1689-1707.

Vonk, J., & Povinelli, D. (2011). Individual differences in long-term cognitive testing in a group of captive chimpanzees. *International Journal of Comparative Psychology, 24*, 137-167.

von Rohr, C. R., van Schaik, C. P., Kissling, A., & Burkart, J. M. (2015). Chimpanzees' bystander reactions to infanticide. *Human Nature*, *26*(2), 143-160.

Waitt, C., & Little, A. C. (2006). Preferences for symmetry in conspecific facial shape among *Macaca mulatta*. *International Journal of Primatology*, *27*(1), 133-145.

Waller, B. M., & Dunbar, R. I. (2005). Differential behavioural effects of silent bared teeth display and relaxed open mouth display in chimpanzees (*Pan troglodytes*). *Ethology, 111*(2), 129-142.

Walum, H., Westberg, L., Henningsson, S., Neiderhiser, J. M., Reiss, D., Igl, W., . . . Lichtenstein, P. (2008). Genetic variation in the vasopressin receptor 1a gene (AVPR1A) associates with pair-bonding behavior in humans. *Proceedings of the National Academy of Sciences of the United States of America, 105*(37), 14153-14156. doi: 10.1073/pnas.0803081105

Watling, R. L., Deitz, J., & White, O. (2001). Comparison of sensory profile scores of young children with and without autism spectrum disorders. *American Journal of Occupational Therapy, 55*, 416-423.

Watson, K. K., & Platt, M. L. (2012). Of mice and monkeys: using non-human primate models to bridge mouse- and human-based investigations of autism spectrum disorders. *Journal of Neurodevelopmental Disorders, 4*(21), 1-10.

Watters, J. V., & Powell, D. M. (2012). Measuring animal personality for use in population management in zoos: suggested methods and rationale. *Zoo Biology, 31*(1), 1-12. doi: 10.1002/zoo.20379

Watts, D. P. (1994). *Behavioral Ecology and Sociobiology, 34*(5), 347-358.

Webb, C. E., Franks, B., Romero, T., Higgins, E. T., & de Waal, F. B. (2014). Individual differences in chimpanzee reconciliation relate to social switching behaviour. *Animal Behaviour*, *90*, 57-63.

Weinstein, P. (1995). *Introductory Biology*. Sydney, Australia: Pascal Press.

Weisberg, S. (2001). Yeo-Johnson Power Transformations. *Department of Applied Statistics, University of Minnesota*.

Weiss, A., Adams, M. J., & King, J. E. (2011). Happier orang-utans live longer lives. *Biology Letters*. doi: 10.1098/rsbl20110543

Weiss, A., Adams, M. J., Widdig, A., & Gerald, M. S. (2011). Rhesus macaques (*Macaca mulatta*) as living fossils of hominoid personality and subjective well-being. *Journal of Comparative Psychology, 125*(1), 72-83. doi: 10.1037/a0021187

Weiss, A., Bates, T. C., & Luciano, M. (2008). Happiness is a personal(ity) thing. The genetics of personality and well-being in a representative sample. *Psychological Science, 19*(3), 205-210.

Weiss, A., Gartner, M. C., Gold, K. C., & Stoinski, T. S. (2013). Extraversion predicts longer survival in gorillas: an 18-year longitudinal study. *Proceedings of the Royal Society B, 280*(1752), 20122231. doi: 10.1098/rspb.2012.2231

Weiss, A., Inoue-Murayama, M., Hong, K. W., Inoue, E., Udono, T., Ochiai, T., . . . King, J. E. (2009). Assessing chimpanzee personality and subjective well-being in Japan. *American Journal of Primatology, 71*(4), 283-292. doi: 10.1002/ajp.20649

Weiss, A., Inoue-Murayama, M., King, J. E., Adams, M. J., & Matsuzawa, T. (2012). All too human? Chimpanzee and orang-utan personalities are not anthropomorphic projections. *Animal Behaviour, 83*(6), 1355-1365. doi: 10.1016/j.anbehav.2012.02.024

Weiss, A., & King, J. E. (2015). Great ape origins of personality maturation and sex differences: A study of orangutans and chimpanzees. *Journal of Personality and Social Psychology, 108*(4), 648-664. doi: 10.1037/pspp0000022

Weiss, A., King, J. E., & Enns, R. M. (2002). Subjective well-being is heritable and genetically correlated with dominance in chimpanzees (*Pan troglodytes*). *Journal of Personality and Social Psychology, 83*(5), 1141-1149.

Weiss, A., King, J. E., & Hopkins, W. D. (2007). A cross-setting study of chimpanzee (Pan troglodytes) personality structure and development: zoological parks and Yerkes National Primate Research Center. *American Journal of Primatology, 69*(11), 1264-1277. doi: 10.1002/ajp.20428

Weiss, A., King, J. E., & Perkins, L. (2006). Personality and subjective well-being in orangutans (*Pongo pygmaeus* and *Pongo abelii*). *Journal of Personality and Social Psychology, 90*(3), 501-511. doi: 10.1037/0022-3514.90.3.501

Weiss, A., Staes, N., Pereboom, J. J., Inoue-Murayama, M., Stevens, J. M., & Eens, M. (2015). Personality in bonobos. *Psychological Science*. doi: 10.1177/0956797615589933

Welker, K. M., Goetz, S. M., & Carré, J. M. (2015). Perceived and experimentally manipulated status moderates the relationship between facial structure and risk-taking. *Evolution and Human Behavior*, *36*(6), 423-429.

Wersinger, S. R., Ginns, E. I., O'Carroll, A. M., Lolait, S. J., & Young, W. S. (2002). Vasopressin V1b receptor knockout reduces aggressive behavior in male mice. *Molecular Psychiatry, 7*, 975-984.

Weston, E. M., Friday, A. E., Johnstone, R. A., & Schrenk, F. (2004). Wide faces or large canines? The attractive versus the aggressive primate. *Proceedings of the Royal Society B: Biological Science,* 271(6), S416-419. doi: 10.1098/rsbl.2004.0203

Weston, E. M., Friday, A. E., & Liò, P. (2007). Biometric evidence that sexual selection has shaped the hominin face. *PLoS ONE*, *2*(8), e710.

Whilde, J., & Marples, N. (2011). The behavior of a zoo-housed infant orangutan after the death of its mother. *Zoo Biology, 30*(2), 205-211. doi: 10.1002/zoo.20329

Whiten, A. (2000). Primate culture and social learning. *Cognitive Science*, *24*(3), 477-508.

Whiten, A. (2011). The scope of culture in chimpanzees, humans and ancestral apes. *Philosophical Transactions of the Royal Society of London B: Biological Sciences, 366*(1567), 997-1007. doi: 10.1098/rstb.2010.0334

Whiten, A., McGuigan, N., Marshall-Pescini, S., & Hopper, L. M. (2009). Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *364*(1528), 2417-2428.

Wielebnowski, N. C., Fletchall, N., Carlstead, K., Busso, J. M., & Brown, J. L. (2002). Noninvasive assessment of adrenal activity associated with husbandry and behavioral factors in the North American clouded leopard population. *Zoo Biology, 21*(1), 77-98. doi: 10.1002/zoo.10005

Wilson, S. F. (1982). Environmental influences on the activity of captive apes. *Zoo Biology, 1*(3), 201-209.

Wilson, V., Lefevre, C. E., Morton, F. B., Brosnan, S. F., Paukner, A., & Bates, T. C. (2014). Personality and facial morphology: Links to assertiveness and neuroticism in capuchins (*Sapajus [Cebus] apella*). *Personality and Individual Differences, 58*. doi: 10.1016/j.paid.2013.10.008

Wilson, V., Weiss, A., Humle, T., Morimura, N., Udono, T., Idani, G., . . . Inoue-Murayama, M. (in press). The heritabilities of chimpanzee personality domains and composites and their associations with arginine vasopressin receptor 1a genotype. *Behaviour Genetics*.

Wilson, V. A. D. & Weiss, A. (2015). Social relationships in nonhuman primates: Potential models of pervasive disorders. In P. L. Roubertoux (Ed.), *Organism Models of Autism Spectrum Disorders*, Neuromethods vol. 100, (pp. 283-302). New York, NY: Springer Science+Business Media.

Wimmer, H., & Perner, J. (1983). Beliefs about beliefs: representation and constraining function of wrong beliefs in young children's understanding of deception. *Cognition, 13*, 103-128.

Wispé, L. (1986). The distinction between sympathy and empathy: To call forth a concept, a word is needed. *Journal of Personality and Social Psychology, 50*(2), 314-321.

Wittig, R. M., Crockford, C., Lehmann, J., Whitten, P. L., Seyfarth, R. M., & Cheney, D. L. (2008). Focused grooming networks and stress alleviation in wild female baboons. *Hormones and Behavior*, *54*(1), 170-177.

Yamamoto, S., Humle, T., & Tanaka, M. (2009). Chimpanzees help each other upon request. *PLoS ONE*, *4*(10), 1-7.

Yeargin-Allsopp, M., Rice, C., Karapurkar, T., Doernberg, N., Boyle, C., & Murphy, C. (2003). Prevalence of Autism in a US Metropolitan Area. *The Journal of American Medical Association, 289*(1), 150-155.

Yerkes, R. M. (1939). The history and personality of the chimpanzee. *The American Naturalist, 73*(745), 97-112.

Zilioli, S., Sell, A. N., Stirrat, M., Jagore, J., Vickerman, W., & Watson, N. V. (2015). Face of a fighter: Bizygomatic width as a cue of formidability. *Aggressive Behavior, 41*(4), 322-330. doi: 10.1002/ab.21544

Appendix A. Supplementary tables from Chapter 2

Table A1

ICCs for personality items in Bolivian and common squirrel monkeys and genus-level *Saimiri*

	Bolivian squirrel monkeys		Common squirrel monkeys		*Saimiri*	
Items	*ICC*(3,1)	*ICC*(3,*k*)	*ICC*(3,1)	*ICC*(3,*k*)	*ICC*(3,1)	*ICC*(3,*k*)
			Personality			
Active	0.53	0.78	0.40	0.64	0.49	0.74
Affectionate	0.20	0.45	0.42	0.67	0.27	0.53
Aggressive	0.35	0.63	0.18	0.38	0.28	0.54
Anxious	0.25	0.51	0.28	0.52	0.26	0.51
Autistic	0.35	0.64	0.58	0.79	0.46	0.72
Bullying	0.28	0.56	0.22	0.43	0.26	0.51
Cautious	0.22	0.48	0.45	0.69	0.34	0.61
Clumsy	0.09	0.23	0.22	0.44	0.11	0.27
Conventional	0.02	0.06	0.00	0.01	0.00	0.01
Cool	0.44	0.72	0.30	0.54	0.40	0.66
Curious	0.15	0.35	0.23	0.45	0.16	0.36
Decisive	0.26	0.53	0.17	0.37	0.23	0.47
Defiant	0.50	0.76	0.31	0.56	0.44	0.70
Dependent-Follower	0.23	0.50	0.43	0.67	0.28	0.53
Depressed	0.15	0.37	0.29	0.53	0.19	0.41
Disorganized	0.06	0.17	0.03	0.08	0.04	0.12
Distractible	0.15	0.37	0.12	0.27	0.13	0.32
Dominant	0.43	0.71	0.27	0.51	0.37	0.63
Erratic	0.07	0.19	0.19	0.40	0.13	0.30
Excitable	0.17	0.40	0.28	0.52	0.20	0.42
Fearful	0.19	0.43	0.20	0.42	0.19	0.42
Friendly	0.05	0.15	0.11	0.25	0.07	0.18
Gentle	0.26	0.53	0.11	0.25	0.21	0.44
Helpful	0.27	0.54	0.23	0.46	0.25	0.50
Imitative	0.04	0.12	0.30	0.54	0.16	0.35
Impulsive	0.16	0.37	0.34	0.59	0.20	0.42
Independent	0.35	0.63	0.26	0.50	0.32	0.59
Individualistic	0.12	0.30	0.33	0.58	0.22	0.46
Innovative	0.16	0.37	0.17	0.37	0.18	0.39

Items	*ICC*(3,1)	*ICC*(3,*k*)	*ICC*(3,1)	*ICC*(3,*k*)	*ICC*(3,1)	*ICC*(3,*k*)
Inquisitive	0.25	0.52	-0.04	-0.11	0.15	0.35
Intelligent	0.19	0.42	0.30	0.54	0.21	0.44
Inventive	0.28	0.55	0.34	0.59	0.29	0.55
Irritable	0.28	0.55	-0.10	-0.32	0.15	0.34
Jealous	0.17	0.40	0.15	0.33	0.16	0.36
Lazy	0.43	0.71	0.11	0.25	0.36	0.63
Manipulative	0.31	0.59	0.27	0.50	0.29	0.55
Persistent	0.29	0.57	0.08	0.18	0.20	0.43
Playful	0.27	0.54	0.29	0.54	0.27	0.53
Predictable	0.10	0.25	0.19	0.39	0.12	0.30
Protective	0.08	0.22	0.27	0.51	0.14	0.32
Quitting	0.01	0.04	0.11	0.26	0.05	0.14
Reckless	0.29	0.56	0.18	0.37	0.24	0.48
Sensitive	0.17	0.39	0.03	0.08	0.10	0.24
Sociable	0.15	0.36	0.20	0.40	0.16	0.36
Solitary	0.37	0.65	0.44	0.69	0.39	0.65
Stable	0.17	0.39	0.06	0.15	0.13	0.31
Stingy-Greedy	0.37	0.65	0.40	0.65	0.39	0.66
Submissive	0.50	0.76	0.22	0.44	0.39	0.66
Sympathetic	0.25	0.51	0.36	0.60	0.29	0.55
Thoughtless	0.43	0.71	0.15	0.32	0.30	0.56
Timid	0.36	0.65	0.29	0.53	0.33	0.60
Unemotional	0.21	0.46	0.20	0.41	0.20	0.42
Unperceptive	-0.03	-0.12	-0.03	-0.07	-0.04	-0.13
Vulnerable	0.40	0.68	0.34	0.58	0.37	0.64
			Well-being			
Mood	0.43	0.71	0.54	0.71	---	---
Social	0.28	0.56	0.49	0.67	---	---
Goals	0.32	0.61	-0.27	-0.78	---	---
Be monkey	0.39	0.67	-5.92E-16	-1.23E-15	---	---

Table A2

Item loadings on well-being component for Bolivian squirrel monkeys

Item	Well-being	h^2
Mood	0.95	0.90
Social	0.58	0.34
Goals	0.85	0.73
Be monkey	0.96	0.92

Table A3

Component structure from Morton Lee, Buchanan-Smith, et al., (2013) for personality items assessed in brown capuchins, *Sapajus apella*

	Item loadings	
Personality component	Negative	Positive
Assertiveness	Submissive Gentle Vulnerable Timid Cautious Dependent/Follower Fearful	Bullying Aggressive Stingy/Greedy Dominant Jealous Irritable Independent Manipulative Reckless
Openness	Conventional Lazy Quitting	Inventive Innovative Inquisitive Playful Active Curious Imitative Persistent Defiant
Neuroticism	Stable Cool Predictable Unemotional Decisive Sympathetic	Excitable Impulsive
Sociability	Solitary Depressed Anxious Autistic	Sociable Affectionate Friendly
Attentiveness	Disorganised Unperceptive Thoughtless Clumsy Distractible Erratic	Helpful

Appendix B. Questionnaires used in Data Collection

MONKEY PERSONALITY TRAIT ASSESSMENT

Monkey personality assessments can be made with this questionnaire by assigning a numerical score for all of the personality traits listed on the fol- lowing pages. Make your judgments on the basis of your own understanding of the trait guided by the short clarifying definition following each trait. The monkey's own behaviours and interactions with other monkeys should be the basis for your numerical ratings. Use your own subjective judgment of typical monkey behaviour to decide if the monkey you are scoring is above, below, or average for a trait. The following seven point scale should be used to make your ratings.

1. Displays either total absence or negligible amounts of the trait.

2. Displays small amounts of the trait on infrequent occasions.

3. Displays somewhat less than average amounts of the trait.

4. Displays about average amounts of the trait.

4. Displays somewhat greater than average amounts of the trait.

6. Displays considerable amounts of the trait on frequent occasions.

7. Displays extremely large amounts of the trait.

Please give a rating for each trait even if your judgment seems to be based on a purely subjective impression of the monkey and you are somewhat unsure about it. Indicate your rating by placing a cross in the box underneath
the chosen number. ☒

Finally, do not discuss your rating of any particular monkey with anyone else. As explained in the handout accompanying this questionnaire, this restriction is necessary in order to obtain valid reliability coefficients for the traits.

MONKEY PERSONALITY TRAIT ASSESSMENT

Monkey's full name: ____

Rater's full name: ____

Date (Mon/Day/Yr): ____

FEARFUL: Subject reacts excessively to real or imagined threats by displaying behaviours such as screaming, grimacing, running away or other signs of anxiety or distress.

Least 1 2 3 4 5 6 7 Most

DOMINANT: Subject is able to displace, threaten, or take food from other monkeys. Or subject may express high status by decisively intervening in social interactions.

Least 1 2 3 4 5 6 7 Most

PERSISTENT: Subject tends to continue in a course of action, task, or strategy for a long time or continues despite opposition from other monkeys.

Least 1 2 3 4 5 6 7 Most

CAUTIOUS: Subject often seems attentive to possible harm or danger from its actions. Subject avoids risky behaviours.

Least 1 2 3 4 5 6 7 Most

STABLE: Subject reacts to its environment including the behaviour of other monkeys in a calm, equable, way. Subject is not easily upset by the behaviours of other monkeys.

Least Most
1 2 3 4 5 6 7

AUTISTIC: Subject often displays repeated, continuous, and stereotyped behaviours such as rocking or self clasping.

Least Most
1 2 3 4 5 6 7

CURIOUS: Subject has a desire to see or know about objects, devices, or other monkeys. This includes a desire to know about the affairs of other monkeys that do not directly concern the subject.

Least Most
1 2 3 4 5 6 7

THOUGHTLESS: Subject often behaves in a way that seems imprudent or forgetful.

Least Most
1 2 3 4 5 6 7

STINGY/GREEDY: Subject is excessively desirous or covetous of food, favored locations, or other resources in the enclosure. Subject is unwilling to share these resources with others.

Least Most
1 2 3 4 5 6 7

JEALOUS: Subject is often troubled by others who are in a desirable or advantageous situation such as having food, a choice location, or access to social groups. Subject may attempt to disrupt activities of advantaged monkeys.

Least Most

1 2 3 4 5 6 7

INDIVIDUALISTIC: Subject's behaviour stands out compared to that of the other individuals in the group. This does not mean that it does not fit or is incompatible with the group.

Least Most

1 2 3 4 5 6 7

RECKLESS: Subject is rash or unconcerned about the consequences of its behaviours.

Least Most

1 2 3 4 5 6 7

SOCIABLE: Subject seeks and enjoys the company of other monkeys and engages in amicable, affable, interactions with them.

Least Most

1 2 3 4 5 6 7

DISTRACTIBLE: Subject is easily distracted and has a short attention span.

Least Most

1 2 3 4 5 6 7

TIMID: Subject lacks self confidence, is easily alarmed and is hesitant to venture into new social or non-social situations.

Least Most

1 2 3 4 5 6 7

SYMPATHETIC: Subject seems to be considerate and kind towards others as if sharing their feelings or trying to provide reassurance.

Least Most

1 2 3 4 5 6 7

PLAYFUL: Subject is eager to engage in lively, vigorous, sportive, or acrobatic behaviours with or without other monkeys.

Least Most

1 2 3 4 5 6 7

SOLITARY: Subject prefers to spend considerable time alone not seeking or avoiding contact with other monkeys.

Least Most

1 2 3 4 5 6 7

VULNERABLE: Subject is prone to be physically or emotionally hurt as a result of dominance displays, highly assertive behaviour, aggression, or attack by another monkey.

Least Most

1 2 3 4 5 6 7

INNOVATIVE: Subject engages in new or different behaviours that may involve the use of objects or materials or ways of interacting with others.

Least Most

1 2 3 4 5 6 7

ACTIVE: Subject spends little time idle and seems motivated to spend considerable time either moving around or engaging in some overt, energetic behaviour.

Least Most
1 2 3 4 5 6 7

HELPFUL: Subject is willing to assist, accommodate, or cooperate with other monkeys.

Least Most

1 2 3 4 5 6 7

BULLYING: Subject is overbearing and intimidating towards younger or lower ranking monkeys.

Least Most
1 2 3 4 5 6 7

AGGRESSIVE: Subject often initiates fights or other menacing and agonistic encounters with other monkeys.

Least Most
1 2 3 4 5 6 7

MANIPULATIVE: Subject is adept at forming social relationships for its own advantage, especially using alliances and friendships to increase its social standing. Monkey seems able and willing to use others.

Least Most

1 2 3 4 5 6 7

GENTLE: Subject responds to others in an easy-going, kind, and considerate manner. Subject is not rough or threatening.

Least Most

1 2 3 4 5 6 7

AFFECTIONATE: Subject seems to have a warm attachment or closeness with other monkeys. This may entail frequently grooming, touching, embracing, or lying next to others.

Least Most

1 2 3 4 5 6 7

EXCITABLE: Subject is easily aroused to an emotional state. Subject becomes highly aroused by situations that would cause less arousal in most monkeys.

Least Most

1 2 3 4 5 6 7

IMPULSIVE: Subject often displays some spontaneous or sudden behaviour that could not have been anticipated. There often seems to be some emotional reason behind the sudden behaviour.

Least Most

1 2 3 4 5 6 7

INQUISITIVE: Subject seems drawn to new situations, objects, or animals. Subject behaves as if it wishes to learn more about other monkeys, objects, or persons within its view.
Least most
1 2 3 4 5 6 7

SUBMISSIVE: Subject often gives in or yields to another monkey. Subject acts as if it is subordinate or of lower rank than other monkeys.

Least Most
1 2 3 4 5 6 7

COOL: Subject seems unaffected by emotions and is usually undisturbed, assured, and calm.

Least Most
1 2 3 4 5 6 7

DEPENDENT/FOLLOWER: Subject often relies on other monkeys for leadership, reassurance, touching, embracing and other forms of social support.

Least Most
1 2 3 4 5 6 7

IRRITABLE: Subject often seems in a bad mood or is impatient and easily provoked to anger exasperation and consequent agonistic behaviour.

Least Most
1 2 3 4 5 6 7

UNPERCEPTIVE: Subject is slow to respond or understand moods, dispositions, or behaviours of others.

Least Most
1 2 3 4 5 6 7

PREDICTABLE: Subject’s behaviour is consistent and steady over extended periods of time. Subject does little that is unexpected or deviates from its usual behavioural routine.

Least Most

1 2 3 4 5 6 7

DECISIVE: Subject is deliberate, determined, and purposeful in its activities.

Least Most

1 2 3 4 5 6 7

DEPRESSED: Subject does not seek out social interactions with others and often fails to respond to social interactions of other monkeys. Subject often appears isolated, withdrawn, sullen, brooding, and has reduced activity.

Least Most

1 2 3 4 5 6 7

CONVENTIONAL: Subject seems to lack spontaneity or originality. Subject behaves in a consistent manner from day to day and stays well within the social rules of the group.

Least Most

1 2 3 4 5 6 7

SENSITIVE: Subject is able to understand or read the mood, disposition, feelings, or intentions of other monkeys often on the basis of subtle, minimal cues.

Least Most

1 2 3 4 5 6 7

DEFIANT: Subject is assertive or contentious in a way inconsistent with the usual dominance order. Subject maintains these actions despite unfavorable consequences or threats from others.

Least Most
1 2 3 4 5 6 7

INTELLIGENT: Subject is quick and accurate in judging and comprehending both social and non-social situations. Subject is perceptive and discerning about social relationships.

Least Most
1 2 3 4 5 6 7

PROTECTIVE: Subject shows concern for other monkeys and often intervenes to prevent harm or annoyance from coming to them.

Least Most
1 2 3 4 5 6 7

QUITTING: Subject readily stops or gives up activities that have recently been started.

Least Most
1 2 3 4 5 6 7

INVENTIVE: Subject is more likely than others to do new things including novel social or non-social behaviours. Novel behaviour may also include new ways of using devices or materials.

Least Most
1 2 3 4 5 6 7

CLUMSY: Subject is relatively awkward or uncoordinated during movements including but not limited to walking, acrobatics, and play.

Least Most

1 2 3 4 5 6 7

ERRATIC: Subject is inconsistent, indefinite, and widely varying in its behaviour and moods.

Least Most

1 2 3 4 5 6 7

FRIENDLY: Subject often seeks out contact with other monkeys for amiable, genial activities. Subject infrequently initiates hostile behaviours towards other monkeys.

Least Most

1 2 3 4 5 6 7

ANXIOUS: Subject often seems distressed, troubled, or is in a state of uncertainty.

Least Most

1 2 3 4 5 6 7

LAZY: Subject is relatively inactive, indolent, or slow moving and avoids energetic activities.

Least Most

1 2 3 4 5 6 7

DISORGANIZED: Subject is scatterbrained, sloppy, or haphazard in its behaviour as if not following a consistent goal.

Least Most

1 2 3 4 5 6 7

UNEMOTIONAL: Subject is relatively placid and unlikely to become aroused, upset, happy, or sad.

Least Most

1 2 3 4 5 6 7

IMITATIVE: Subject often mimics, or copies behaviours that it has observed in other monkeys.

Least Most

1 2 3 4 5 6 7

INDEPENDENT: Subject is individualistic and determines its own course of action without control or interference from other monkeys.

Least Most

1 2 3 4 5 6 7

ASSESSMENT OF SUBJECTIVE WELL-BEING IN MONKEYS

This questionnaire has four questions, all relating to the subjective well-being of the monkeys at your site. Each question asks about a different personality dimension or trait relating to subjective well-being. The following scale should be used to make your ratings.

1. Displays either total absence or negligible amounts of the trait.

2. Displays small amounts of the trait on infrequent occasions.

3. Displays somewhat less than average amounts of the trait.

4. Displays about average amounts of the trait.

5. Displays somewhat greater than average amounts of the trait.

6. Displays considerable amounts of the trait on frequent occasions.

7. Displays extremely large amounts of the trait.

Please give a rating for each trait even if your judgment seems to be based on a purely subjective impression of the monkey and you are somewhat unsure about it. Indicate your rating by placing a cross in the box underneath the chosen number. ☒

Finally, do not discuss your rating of any particular monkey with anyone else. As explained in the handout accompanying this questionnaire, this restriction is necessary in order to obtain valid reliability coefficients for the traits.

ASSESSMENT OF SUBJECTIVE WELL-BEING IN MONKEYS

Monkey's full name: ______________________________

Rater's full name: ______________________________

How long have you known the monkey? ____________________

Years: ______________________________

Months: ______________________________

Date (Mon/Day/Yr): ______________________________

Estimate the amount of time the monkey is happy, contented, enjoying itself, or otherwise in a positive mood. Assume that at other times the monkey is unhappy, bored, frightened, or otherwise in a negative mood.

Least Most

1 2 3 4 5 6 7

Estimate the extent to which social interactions with other monkeys are satisfying, enjoyable experiences as opposed to being a source of fright, distress, frustration, or some other negative experience. It is not the number of social interactions that should be estimated, but the extent to which social interactions that do occur are a positive experience for the monkey. Use as many social interactions that you can recall as a basis for your judgment.

Least Most

1 2 3 4 5 6 7

Estimate, for this monkey, the extent to which it is effective or successful in achieving its goals or wishes. Examples of goals would be achieving desired locations, devices, or materials in the environment. Keep in mind that each monkey will presumably have its own set of goals that may be different from other monkeys.

Least Most

1 2 3 4 5 6 7

Imagine how happy you would be if you were that monkey for a week. You would be exactly like that monkey. You would behave the same way as that monkey, would perceive the world the same way as that monkey, and would feel things the same way as that monkey.

Least Most

1 2 3 4 5 6 7

Appendix C. Supplementary tables from Chapter 5

Table C1

Event descriptions and categories from behavioural observations

Description	Event category
Barks/Screams	Conflict
Fight	
Fight (chase)	
Fight/Hoots/Screams	
Hoots/Scream	
Screams	
Screams, Roar	
Screams/Barks	
Screams/Fight	
Screams/Hoots	
Screams/Submissive barks	
Soft screams	
Bang/Hoot	Display
Banging	
Barks (and drumming)	
Display	
Barks/Display	
Display (banging and swaying)	
Display (banging)	
Display (banging)/Barks	
Display (bipedal swaying)	
Display (building, swinging)	
Display (drumming)	
Display (just swaying)	
Display (swayed and hooted)	
Display (swaying)	
Display (swinging)	

Display/Hoots	
Drumming	
Hoots (and banging)	
Hoots/Display	
Submissive barks/Drumming	
Swinging	
Display/Barks/Screams	Display & Conflict
Display (swaying)/Screams	
Fight/Display	
Display/Fight	
Display/Screams	
Display (chasing)	
Display (bipedal swaying)/Screams	
Screams (and bangs)	
Screams/Banging	
Screams/Display	
Barks/Hoots	Hoots
Hoot (soft)	
Hoots	
Hoots (and swaying to Kilimi)	
Hoots (building)	
Hoots (slightly)	
Hoots, Barks	
Hoots/Grunts	
Hoots/Submissive barks	
Pant-roar	
Submissive barks	Other
waa-barks	

Note. '/' indicates separate behaviours treated as one event. If description included 'scream', 'chase' or 'fight' this was categorised as Conflict. If description included 'bang', 'drum', 'swing' or 'display' this was categorised as Display. If description included any combination of 'scream', 'chase' or 'fight' with 'bang', 'drum', 'swing' or 'display' this was categorised as Display and Conflict. If description included 'hoots' with no accompanying behaviours that designated the event as Display/Conflict, then it was categorised as Hoots. If the description included 'submissive barks' or 'waa-barks' with no accompanying behaviours that designated the event as Display/Conflict or Hoots, then it was categorised as Other.

Table C2

Dates and times of behavioural observations for all chimpanzees

Chimp	DA	PE	CI	LI	LO	KL	KD	PA	FK	Q	RE	ED	LB	SO	LU	EM	HL	EV
Week 1	13.01	13.01	13.01	13.01	13.01	13.01	16.01	16.01	16.01	16.01	16.01	17.01	17.01	17.01	17.01	17.01	17.01	17.01
Time	09:50	10:32	11:05	13:00	13:30	14:00	12:46	13:20	13:55	14:33	15:10	09:35	10:10	11:00	11:50	12:20	13:16	13:47
Week 2	30.01	27.01	27.01	27.01	30.01	30.01	31.01	*27.01*	31.01	31.01	27.01	31.01	30.01	31.01	31.01	27.01	30.01	30.01
Time	14:30	14:15	12:30	13:43	14:00	15:05	13:59	13:00	11:16	12:36	15:00	10:42	12:37	12:02	13:26	15:30	11:45	13:03
Week 3	06.02*	03.02	06.02	03.02	03.02	06.02	07.02	06.02	07.02	07.02	06.02	07.02	03.02	06.02	03.02	07.02	07.02	06.02
Time	11:11	11:21	09:45	14:28	13:57	12:17	11:56	13:51	14:00	14:36	11:41	11:22	13:10	12:51	12:40	12:30	13:00	14:27
Week 4	17.02	17.02	21.02	17.02	20.02	17.02	21.02	20.02	20.02	17.02	21.02	21.02	20.02	20.02	17.02	20.02	21.02	21.02
Time	11:58	14:15	12:50	11:25	13:40	13:00	11:30	14:05	10:40	13:40	12:10	09:20	12:20	11:50	14:45	11:15	09:50	10:40
Week 5	24.02	27.02	24.02	27.02	24.02	27.02	28.02	28.02	27.02	28.02	28.02	27.02	24.02	28.02	24.02*	24.02	28.02	27.02
Time	11:43	11:20	13:40	13:25	13:00	14:00	11:30	14:30	12:10	14:00	12:50	10:50	12:30	12:00	14:20	14:50	13:20	12:40
Week 6	06.03*	04.03	04.03	06.03*	07.03	07.03	07.03	04.03	07.03	06.03	06.03	04.03	04.03	07.03	04.03	06.03	07.03	06.03
Time	11:00	13:12	11:12	10:30	13:50	12:32	11:25	12:30	14:20	13:30	12:10	11:50	10:40	13:00	13:45	13:00	12:00	11:40
Week 7	10.03	13.03	13.03	13.03	14.03	14.03	14.03	14.03	13.03	14.03	14.03	10.03	10.03	14.03	13.03	10.03	13.03	10.03
Time	14:05	12:14	11:35	13:40	13:50	10:45	12:30	11:55	14:10	11:20	14:25	15:10	14:35	13:20	12:45	12:40	11:05	13:10
Week 8	21.03	21.03	*21.03*	17.03	20.03	17.03	21.03*	17.03	17.03	20.03	20.03	17.03	20.03	20.03	20.03	21.03	20.03	21.03
Time	09:40	12:20	10:40	11:25	13:37	12:00	10:10	13:30	14:10	10:20	14:45	15:00	13:10	11:28	14:14	13:10	10:50	14:20
Week 9[+]	22.09	23.09	22.09	23.09	22.09	25.09	23.09	23.09	23.09	22.09	25.09	22.09	25.09	22.09	25.09	25.09	25.09	23.09
Time	12:40	11:15	14:00	14:00	14:40	12:35	12:40	14:32	13:14	11:22	14:10	12:05	14:57	15:10	15:25	12:05	13:40	11:17
Week 10	30.09	30.09	02.10	30.09	03.10	03.10	30.09	02.10	02.10	03.10	03.10	02.10	02.10	03.10	02.10	30.09	30.09	03.10
Time	13:00	11:40	13:46	13:44	13:55	14:32	12:20	13:22	09:40	15:00	13:15	10:15	12:15	12:00	09:00	11:10	14:14	11:30
Week 11	10.10	07.10	07.10	07.10	07.10	10.10	06.10	09.10	10.10	09.10	10.10	09.10	10.10	10.10	07.10	07.10	09.10	06.10

Chimp	DA	PE	CI	LI	LO	KL	KD	PA	FK	Q	RE	ED	LB	SO	LU	EM	HL	EV
Time	13:20	11:44	12:40	14:50	12:10	15:00	16:00	10:35	12:46	12:50	13:55	16:00	12:12	10:30	15:25	11:05	13:20	13:00
Week 12	13.10	---	17.10	14.10	13.10	16.10	17.10	17.10	16.10	17.10	14.10	17.10	14.10	14.10	14.10	17.10	14.10	14:10
Time	16:05	---	14:00	11:50	10:35	10:45	15:05	10:45	16:00	12:20	10:43	14:35	11:17	15:40	12:28	11:15	14:30	15:10
Week 13	---	20.10	---	---	---	---	---	---	---	---	---	---	---	---	21.10	---	---	---
Time	---	16:10	---	---	---	---	---	---	---	---	---	---	---	---	10:40	---	---	---

Note. *Focal cut short. Observation took place in week 13, not week 12. $^{+}$Week 9: HL had 3 month old infant at start of week 9. PA week 2 and CI week 8 (italicised) were not included in analyses.

Appendix D. Publications

Facial Width-To-Height Ratio Relates to Alpha Status and Assertive Personality in Capuchin Monkeys

Carmen Emilia Lefevre[1]*, Vanessa A. D. Wilson[2,3], F. Blake Morton[3,4], Sarah F. Brosnan[5], Annika Paukner[6], Timothy C. Bates[2]*

1 Centre for Decision Research, Leeds University Business School, Leeds, United Kingdom, **2** Department of Psychology, University of Edinburgh, Edinburgh, United Kingdom, **3** Scottish Primate Research Group, Edinburgh, United Kingdom, **4** Behaviour and Evolution Research Group, Psychology, School of Natural Sciences, University of Stirling, Stirling, United Kingdom, **5** Department of Psychology and Language Research Centre, Georgia State University, Atlanta, Georgia, United States of America, **6** Laboratory of Comparative Ethology, Eunice Kennedy Shriver National Institute of Child Health and Human Development, National Institutes of Health, Department of Health and Human Services, Poolesville, Maryland, United States of America

Abstract

Social dominance hierarchies play a pivotal role in shaping the behaviour of many species, and sex differences within these hierarchies often exist. To date, however, few physical markers of dominance have been identified. Such markers would be valuable in terms of understanding the etiology of dominant behaviour and changes in social hierarchies over time. Animals may also use such traits to evaluate the potential dominance of others relative to themselves (i.e. a physical "cue"). Facial width-to-height ratio (fWHR), for example, has been suggested as a cue to dominance in humans, with links to both dominant behaviour and the perception of dominance in other individuals. Whether this association is present in non-human animals is currently not known. Therefore, here we examine within-species links between fWHR and dominant behaviour in 64 brown capuchin monkeys (*Sapajus spp.*) aged between 2 and 40 years. fWHR was positively associated with alpha status and with a dimensional rating of assertive personality in both males and females. Moreover, fWHR showed significant sexual dimorphism in adults but not juveniles, suggesting a developmental change may occur during puberty. In a sub-sample, sex differences were mediated by weight, suggesting fWHR dimorphism does not exceed what would be expected by differences in body weight. This is the first report of an association between face shape and behaviour in a non-human species. Results are discussed in terms of the role that face-behaviour associations might play within capuchin societies, and the possible selective forces that might have led to the evolution of fWHR-dominance associations in humans.

Citation: Lefevre CE, Wilson VAD, Morton FB, Brosnan SF, Paukner A, et al. (2014) Facial Width-To-Height Ratio Relates to Alpha Status and Assertive Personality in Capuchin Monkeys. PLoS ONE 9(4): e93369. doi:10.1371/journal.pone.0093369

Editor: Cédric Sueur, Institut Pluridisciplinaire Hubert Curien, France

Received June 27, 2013; **Accepted** March 4, 2014; **Published** April 4, 2014

Funding: The authors have no support or funding to report.

Competing Interests: The authors have declared that no competing interests exist.

* E-mail: carmenlefevre@me.com (CEL); tim.bates@ed.ac.uk (TCB)

Introduction

In many species, competitive inter- and intra-group encounters between rivalling individuals are common and typically aggressive (e.g. [1,2]). Nonetheless, few external physical measures have been identified to date that appear to mediate these behavioural traits across and within species. For instance, species-level differences in canine size are associated with the frequency and costs of contest competition (e.g. [1]), while body size has been linked to social rank in various species, including, for instance, primates (e.g. [3,4]) and elephant seals [5]. Additional quantifiable physical traits linked to social rank or assertive behaviour would be valuable as these may facilitate a better understanding of the etiology of dominance in animals, including humans. Accordingly, here we report on a candidate cue to dominant behaviour, the facial width-to-height ratio (fWHR), in brown capuchin monkeys (*Sapajus spp.*; hereafter referred to as *Sapajus*; see [6] for recent taxonomy change). Like humans, in which fWHR has been related to dominance behaviours [8–12], *Sapajus* exhibit low canine dimorphism and are therefore an ideal non-human primate species in which to test the relationship between fWHR and correlates of dominance. fWHR was first assessed with attention to its sexual dimorphism in a range of primate species including *Sapajus* [7]. Weston et al. [7] reported an association between fWHR and canine size dimorphism, whereby species with large sexual dimorphism in canine size exhibit less sexual dimorphism in fWHR [7]. Importantly, however, Weston et al. [7] only discussed relative size differences between males and females (i.e. sexual dimorphism) within one species, but not overall size or size differences between species for either fWHR or canine height. Following this initial work, a range of studies, thus far conducted exclusively in humans, have found associations between fWHR and behaviours related to the acquisition of social status. For example, in human males higher fWHR is associated with deception [8], achievement striving [9], decreased rates of reciprocation in economic games [10], increased rates of self-sacrifice for the in-group [11], and, of particular interest here, elevated aggression [12], although the size and robustness of the latter effect is somewhat unclear [13,14]. In addition, several studies of humans have shown that fWHR is related to the perceived dominance and dominance-linked behaviours of others, suggesting that fWHR may serve as a physical cue to one's status within a group [10,15,16]. It is currently unclear, however, whether fWHR is linked to behaviours associated with dominance linked traits in other animals. Here, in order to address this question, we test whether fWHR in *Sapajus* is associated with alpha status and a dimensional rating of assertive personality (hereafter "Assertiveness"; Morton et al. 2013). Testing the link between fWHR and status/Assertiveness in a nonhuman primate species may help with understanding the biological and evolutionary bases of fWHR-dominance relationships in humans.

Sexual Dimorphism in fWHR

Masterson [17] reported consistent sex differences in bizygomatic breadth in adult, but not juvenile, *Sapajus*. Also, as noted above, Weston et al. [7] reported a reciprocal relationship between dimorphism in fWHR and canine size across primate species. *Sapajus*, while having relatively large canines, show little sexual dimorphism in this trait and therefore would be predicted to show significant dimorphism in fWHR, as was found by Weston et al. [7]. However, there are outliers to this trend. For instance, while initial reports indicated that fWHR was dimorphic in humans [12,18], larger studies suggest a lack of dimorphism for this trait (e.g. [14,19,20]). Thus, humans lack significant dimorphism in fWHR and show minimal dimorphism in canine size [21], suggesting that canine size dimorphism may not fully account for species differences in fWHR dimorphism.

Our hypotheses with respect to dimorphism were as follows: Firstly, both studies that previously assessed sex differences in facial width in *Sapajus* [7,17] measured fWHR from the skull. However, these measures may not be informative with respect to the signalling power of fWHR if they do not translate to the skin surface. Therefore, we wished to replicate findings for *Sapajus* fWHR using measurements taken from the skin surface. These incorporate not only skull, but also muscle and soft tissue differences affecting fWHR, thereby reflecting the visible phenotype of fWHR. Additionally, theory concerning dominance cues in humans suggests a link between dominant behaviour and testosterone (e.g. [22]), with a pubertal spike in testosterone and consequent changes in morphology and behaviour [23,24]. Such developmental changes may also occur for human fWHR given its association with adult levels of testosterone [25]. We therefore hypothesized, that this skin-surface measure of fWHR would also be sexually dimorphic in *Sapajus*, with males having higher fWHR than females, as reported by Weston et al. [7] for skull measures. Secondly, based on testosterone effects in puberty and in line with findings by Masterson [17], we hypothesised that sex differences in *Sapajus* fWHR would exist among sexually mature, but not sexually immature, individuals.

fWHR and Dominant Behaviour in Sapajus

Sapajus live in relatively small female-bonded arboreal groups [26,27] that typically include multiple male members [28] as well as both a dominant alpha male and an alpha female [29], with the alpha male being higher-ranking than the alpha female. Cross-species analyses of primates, including capuchins, suggest that such social conditions contribute to lower rates of agonism among conspecifics, and favour facial displays over contact aggression [30]. Indeed, dominance hierarchies in *Sapajus* are, in general, less clearly defined than in Old World primates (e.g. baboons [*Papio spp.*] and rhesus macaques [*Macaca mulatta*]; [31,32]) and at least among captive capuchin groups, it is difficult to place individuals into discrete dominance ranks given their relatively low rates of aggression and high levels of social tolerance compared to other primate species [32]. Although the alpha male and alpha female are normally easy to identify within *Sapajus* groups, the exact ranking of subordinates is usually less certain, with some studies reporting clear linear hierarchies among *Sapajus*, while others do not [26]. This indicates that *Sapajus* are relatively tolerant of having others in close proximity, and thus may live in more flexible societies compared to many other primate species. Taken together with findings in humans, who (like *Sapajus*) are low on canine dimorphism [21], fWHR may reflect individual differences in dominant behaviour in *Sapajus*, and may even substitute for canine size as a physical cue to one's capacity for being more (or less) dominant over other individuals. Thus, we predicted that fWHR is associated with alpha status and Assertiveness in this species. Moreover, based on human studies [8,12] and given that *Sapajus* live in multi-male groups and have flexible dominance hierarchies (factors predicted by Weston et al. [7] to favour reduced canine dimorphism and increased fWHR), we predicted that associations between fWHR and alpha status/Assertiveness in *Sapajus* would hold for both males and females. Lastly, while human fWHR is relatively independent of height and weight [18], several studies indicate that controlling for such body size differences can potentially create artificial links between fWHR and dominant behaviour [20,34,33]. We therefore predicted that overall body size partially mediates the relationship between fWHR and alpha status/Assertiveness in *Sapajus*.

Method

Ethics Statement

This study was non-invasive, and was approved by the local ethics committees from each research site (Animal Care and Use Committee, NICHD; the Research Committee at Living Links, the Animal Care and Use Committee, GSU), and the Psychology Ethics Committee of the University of Stirling. The study was carried out in strict accordance with the recommendations of the "Guidelines for the treatment of animals in behavioural research and teaching" given by the Association for the Study of Animal Behaviour [35], and the NC3R's Guidelines for "Primate accommodation, care and use" [36].

Sample

The sample consisted of a total of 64 individuals (29 female, mean age 12.9 SD = 10.1 years; 35 male, mean age 9.1 SD = 8.6 years) stemming from 7 social groups and a further 4 pair-housings across three sites: The 'Living Links to Human Evolution' Research Centre [34] of the University of St Andrews, in Edinburgh Zoo (6 female, mean age 8.2±4.0 years; 10 male, mean age 11.4±13.4 years), the Language Research Center, Georgia State University (13 female, mean age 15.3±11.8 years; 9 male, mean age 10.9±5.80 years), and the Laboratory of Comparative Ethology at the National Institutes of Health, Poolesville, Maryland (10 female, mean age 12.8±9.20 years; 16 male, mean age 6.6±4.50 years). Infants less than one year old were excluded and age was scored by year of life. The sample was additionally categorised according to whether individuals were adult or juvenile. Following [26], adulthood was defined using the criterion of age $\geq$6 years yielding a sample of 43 adults (with 21 animals classified as juveniles). For a subset of the US individuals, body weight information was available (N = 46, 34 adult). Therefore, we could test for interactions between weight and fWHR among these individuals.

Site Descriptions

Living links, edinburgh zoo. Sixteen capuchins were from the 'Living Links to Human Evolution' Research Centre at the Royal Zoological Society of Scotland, Edinburgh Zoo, UK [37]. These individuals were from two breeding groups, and each cohabited with a group of common squirrel monkeys (*Saimiri* *sciureus*). At the time of this study, the 'East' group ranged from 2–3 adult males, 3 adult females, 3 juveniles, and 0–5 infants. The 'West' group ranged from 2 adult males, 3 adult females, 4–5 juveniles, and 2–5 infants. All monkeys were captive born except the two eldest males, which were likely wild-born and came to Living Links as established members of the groups. One individual was hand-reared. Both groups were housed in 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, providing ample opportunity to engage in natural behaviors. All subjects received commercial TrioMunch pellets supplemented with fresh fruits and vegetables three times daily, and were given cooked chicken and hardboiled eggs once every week. Water was available to the monkeys *ad libitum* at all times and all individuals had full access to proper veterinary care when needed. Further details of housing and husbandry are provided in Leonardi et al. [38].

Language research center, georgia state university. Twenty-two capuchins came from three groups at the Language Research Center of Georgia State University (GSU) in Atlanta, Georgia, USA. The first group consisted of 2 adult males, 2 adult females, 2 juveniles, and 0 infants. The second group consisted of 1 adult male, 2 sub-adult males, 2 adult females, 1 juvenile, and 0 infants and the third group consisted of 2 adult males, 8 adult females, and 0 juveniles or infants. All monkeys were captive born. For all groups, enclosures consisted of an indoor room (first group: 75.84 m^3; second group: 54.42 m^3, third group: 13.28 m^2) connected to a large outdoor enclosure (first group: 13.51 m^2; second group: 21.15 m^2, third group: 55.74 m^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 behavioral testing and all individuals had full access to proper veterinary care when needed. 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 and third housing group had previously been housed together in various combinations at Yerkes National Primate Research Center, before being relocated to GSU 5 years and 1 year ago respectively.

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 1 adult male, 4 adult female and 4 juveniles (2 female and 2 male). 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 1 adult male, 2 adult females, and 4 juveniles (1 female and 3 male). A further nine animals were pair-housed in cages; two pairs and a group of 3 animals were sub-adult to adult males, and one pair was an adult female with a juvenile male. 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 (6.9×4.1×2.1 m each) which were connected via sliding doors. Runs were furnished with swings, ladders and various platforms. Cage-housed monkeys were housed in quad cages (1.63×1.63×.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* and all individuals had full access to proper veterinary care when needed.

fWHR Measures

Measures were based on frontal facial photographs. Prior to measurement, photographs were aligned and scaled according to interpupillary distance. fWHR was then computed as the ratio of bizygomatic-width (maximum horizontal distance from the left to the right facial boundary) to upper face height (vertical distance from the mid-point of the upper lip to the highest point of the eyelids; see Figure 1) using Psychomorph [39]. Measurement reliability was good (ICC = .86) based on a subset of photographs (N = 18) measured twice. In addition, measures from several photographs per individual (mean = 4.69, SD = 2.44) were averaged in order to maximise the signal to noise ratio. All images were taken within 1 calendar year, thus controlling for longitudinal changes. At the time of measurement, the researcher was blind to the assertiveness levels or alpha status of the individuals that were measured.

Alpha Status and Assertiveness Measures

Alpha status. Alpha status was assessed by observation of behaviours including wariness of other group members, being sought out for mating, number of offspring, frequent grooming, and ability to take food from humans and other monkeys (see [32]). In capuchins, the highest-ranking individual is recognised as having alpha status, which in addition to being dominant is also associated with several traits including assertiveness, unprovoked deference by subordinates, central position in the main party of the group and, at least in the wild, a leadership role in group-movements. The combination of these traits allow for easy and

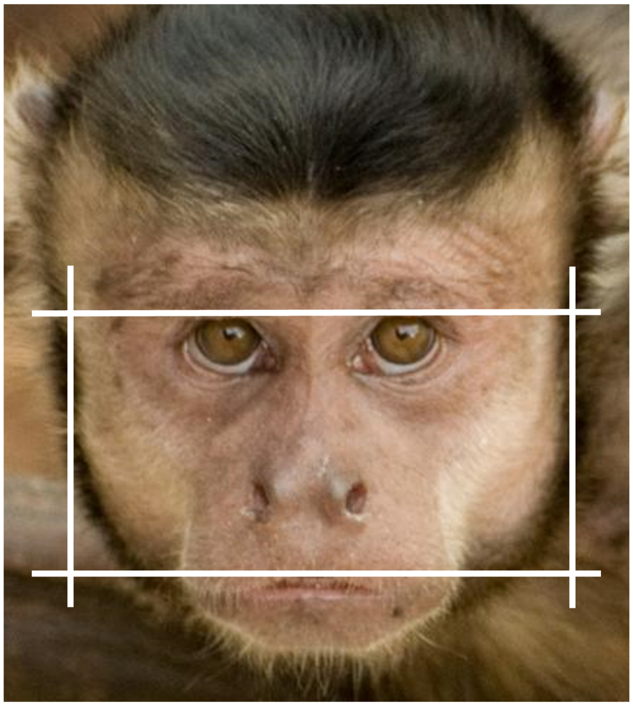


Figure 1. Illustration of the facial width-to-height ratio: zygomatic width (distance between vertical lines) divided by upper face height (distance between horizontal lines).
doi:10.1371/journal.pone.0093369.g001

straight-forward recognition of alpha status in capuchins. Within each social group, one male and one female were accorded alpha status, yielding a total of 18 alpha individuals. The alpha-status of each individual was indicated by a number of raters, and there was complete inter-rater agreement for alpha status assignment. Raters had at least one year of experience working with the monkeys from their site. Alpha status was furthermore related to objective measures of social rank as well as Assertiveness (see next section for details).

Individual differences in assertive personality. Assertiveness was assessed using the Hominoid Personality Questionnaire [40]. Details of this analysis can be found in Morton et al. [33]. Briefly, 127 study subjects (64 of which were also used in the present study) were rated on 54 items by researchers and handlers familiar with the individuals being rated ($X+SD = 3.24+1.61$ raters). Subjects were rated on each adjective, using a 7-point scale ranging from 1 (no expression) to 7 (high expression). Each item consisted of an adjective paired with 1–3 sentences defining it within the context of primate behaviour. For instance, *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". Reliability of ratings within and across raters was good ($ICC+SD = .63+0.14$), therefore all raw ratings were entered into a Principle Components Analysis. Five components were identified from these ratings: Assertiveness, Openness, Neuroticism, Sociability, and Attentiveness. Individual t-scores were calculated for each monkey on each of the five personality dimensions, and these scores predicted relevant behaviour up to one year later (e.g. scores on Sociability positively correlated with time each monkey spent in close proximity to others [33]). Thus, ratings were considered to be valid measures of real-world behaviour among the study subjects.

Here we use individual scores on Assertiveness as a measure of dominance-linked behaviour in our 64 subjects. The highest loadings for this dimension were bullying (.93), aggressive (.92), and dominant (.91) (see table 1 for full component structure) [33]. Assertiveness was positively correlated with behaviours typical of dominance in *Sapajus* (e.g. time spent grooming and aggressing others; [32,33]). Assertiveness was also positively associated with alpha status, in both males ($t_{33} = 6.69$, $p<0.001$, 95% CI [1.04, 1.96]) and females ($t_{25.6} = 5.35$, $p<0.001$, 95% CI [0.90, 2.02]) indicating that this factor captured behaviour relevant to their dominance hierarchy. There was no difference between sexes for Assertiveness scores ($t_{41} = 1.03$, $p = 0.31$), suggesting relatively low sexual differentiation on this trait, but also reflecting possible rater biases towards rating individuals within sex categories. Assertiveness was validated as a measure relevant to status in a sub-sample of individuals for which social rank data were available (N = 18); Assertiveness was strongly correlated with social rank in these monkeys ($r = .67$, $p<.01$), which was calculated using data on the number of aggressive displays given/received by each individual (i.e. David's scores; see [41]).

Statistical Analyses

Potential differences in age, sex ratio, fWHR and Assertiveness between sites were assessed using ANOVA. We tested possible sexual dimorphism in fWHR and relationships to adulthood using ANOVA. We tested the hypothesis that fWHR undergoes age-related changes focused around puberty by performing a linear regression between fWHR and age (in years). We assessed whether fWHR was predictive of alpha status and Assertiveness in adults using a logistic regression. Because we also hypothesised sexual dimorphism, sex and the interaction of sex × age were included as covariates. To test whether weight mediated sex differences in adults, a regression analysis and bootstrapping were conducted with weight as mediator, sex as a predictor and fWHR as the outcome variable. All statistical analyses were performed in R version 2.15 [42], with alpha set at 0.05, two-tailed. The raw data used for analyses can be found in the supporting information.

Results

There were no significant differences between sites for either age ($F_{2,61} = 1.4$, $p = .25$, $\eta_p^2 = .04$), sex ($F_{2,61} = 1.27$, $p = .29$, $\eta_p^2 = .04$), fWHR ($F_{2,61} = 0.28$, $p = .76$, $\eta_p^2 = .01$) or Assertiveness ($F_{2,61} = 0.23$, $p = .79$, $\eta_p^2 = .01$). Data were therefore collapsed across the three sites.

The first hypotheses tested were that fWHR would be sexually dimorphic in *Sapajus* [6], and, that this dimorphism would emerge only in mature individuals following testosterone exposure at puberty. To test this, fWHR in male and female subjects was contrasted using ANOVA. There was no significant sex difference in fWHR across the whole sample ($F_{1,62} = 2.15$, $p = .15$ $\eta_p^2 = .03$). We next tested sex differences independently in adult and juvenile groups. Among adults, i.e. individuals who were six years or older, ($F_{1,41} = 7.70$, $p = .008$, $\eta_p^2 = .16$), males ($M = 2.28$ $SD = 0.18$) showed higher fWHR than females ($M = 2.14$ $SD = 0.14$). By contrast, there were no significant difference in fWHR between male ($M = 2.11$ $SD = 0.10$) and female ($M = 2.14$ $SD = 0.13$) juveniles ($F_{1,19} = .427$, $p = .52$, $\eta_p^2 = .02$). To assess whether the sex difference in adult individuals was linked to developmental changes of fWHR, we tested continuous effects of age on fWHR using regression models, entering fWHR as the dependent variable, with sex, age, and the interaction of sex × age as predictors. Both the main effect of sex ($\beta = 0.38$, $p = .03$) and the interaction of sex × age ($\beta = -0.77$, $p<.001$) were significant, while age effects did not reach significance ($\beta = 0.08$, $p = .47$; overall model: $F_{3,60} = 8.13$, $p<.001$, $R^2 = .29$; Figure 2).

To ensure that developmental status × sex effects on fWHR were related to pubertal developmental changes in fWHR and dominance rank, rather than being influenced by changes specific to old-age, the regression analysis was replicated excluding all 9 animals over 20 years of age. Age effects now reached significance ($\beta = 0.50$, $p<.001$) with sex × age ($\beta = -0.70$, $p = .005$) and sex ($\beta = 0.46$, $p = .06$) remaining predictors (although marginally for sex) in this reduced sample (overall model: $F_{3,51} = 8.40$, $p<.001$, $R^2 = .33$).

Hypothesized mediation effects of weight on sex differences in adults [20] were tested in the sub-sample of adults that had weight data available (N = 34) following Preacher and Hayes' [43] model. The analysis showed a significant relationship (a) between sex and weight ($\beta = -1.24$, $p<.001$), (b) between weight and fWHR ($\beta = 0.09$, $p = .002$), and (c) between sex and fWHR ($\beta = -0.15$, $p = .01$); this relationship disappeared after controlling for weight ($\beta = -0.03$, $p = .57$). Bootstrapping suggested significant mediation (indirect effect = −0.12, CI[-.21,-.01]; Figure 3).

We next moved to test the relationship between fWHR and dominant behaviour, our core hypothesis. Hypothesis three predicted that fWHR would be associated with alpha status and Assertiveness. Since only adult individuals can gain alpha status, this prediction was tested in the adult sample only. An initial independent t-test revealed that alpha individuals had significantly larger fWHR compared to adult non-alpha individuals ($t(41) = 3.45$, $p = .001$). To further investigate this relationship, we next ran a logistic regression, with age and sex as control variables. In this test, fWHR ($\beta = 7.86$, $p = .008$) significantly predicted alpha status (overall model: $X^2_3 = 15.89$, $p = .001$; *Nagelkerke* $R^2 = .42$), controlling for sex ($\beta = -0.72$, $p = .37$) and

Table 1. Salient loadings of assessed personality attributes on Assertiveness, adapted from Morton and colleagues [32].

Trait	Assertiveness Component Loading
Bullying	0.92
Aggressive	0.91
Stingy/Greedy	0.88
Dominant	0.83
Jealous	0.82
Irritable	0.67
Independent	0.61
Manipulative	0.59
Reckless	0.53
Defiant	0.48
Anxious	−0.49
Fearful	−0.57
Dependent/Follower	−0.63
Cautious	−0.67
Timid	−0.68
Vulnerable	−0.75
Gentle	−0.81
Submissive	−0.89

doi:10.1371/journal.pone.0093369.t001

age ($\beta = 0.09$, $p = .04$). The association further held when weight was entered as an additional control variable for the subset of individuals that had weight data available: alpha status was significantly predicted by fWHR ($\beta = 7.09$, $p = .03$) with no other variable reaching significance (all $p > .09$; overall model: $X^2_4 = 10.93$, $p = .03$).

In order to assess whether the differences between alpha and non-alpha fWHR could be accounted for by a physiological response to gaining alpha status, we further assessed whether Assertiveness among all adult animals was predicted by fWHR when controlling sex and age (Figure 4). The overall model was significant ($F_{3,39} = 5.49$, $p = .003$, $R^2 = .30$). Within this, Assertiveness was significantly predicted by fWHR ($\beta = 0.55$, $p = .001$) but not by sex ($\beta = 0.07$, $p = .66$) or age ($\beta = -0.07$, $p = .62$). To test whether this association was exclusively driven by alpha individuals, we next assessed whether fWHR predicted Assertiveness in non-alpha adult individuals. The association between Assertiveness and fWHR remained significant following this restriction (fWHR: $\beta = 0.43$, $p = .05$). In the juveniles, there was no association between Assertiveness and fWHR ($\beta = 0.01$, $p = .97$);

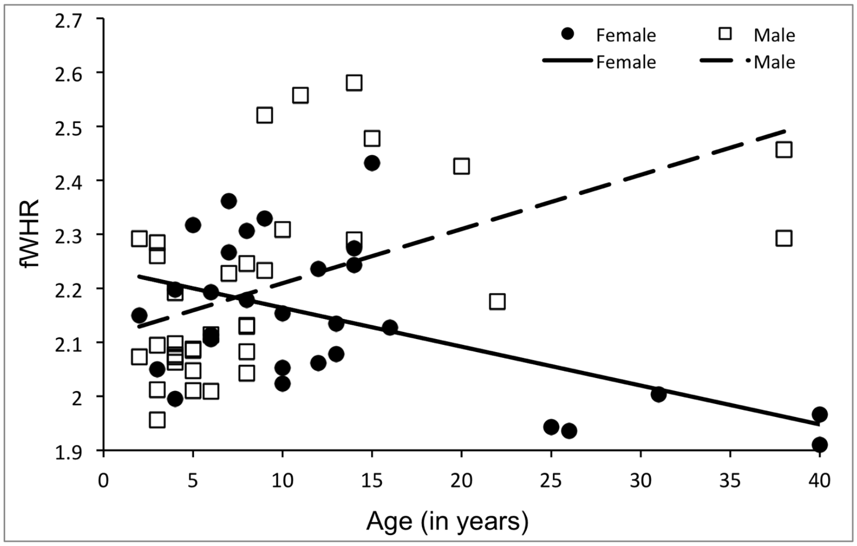


Figure 2. Linear effects of age and sex on fWHR. In males, fWHR increases significantly with age, suggesting developmental changes at puberty. In females, fWHR appears to decrease over the lifespan, although no significant change is observed when excluding animals older than 20 years.
doi:10.1371/journal.pone.0093369.g002

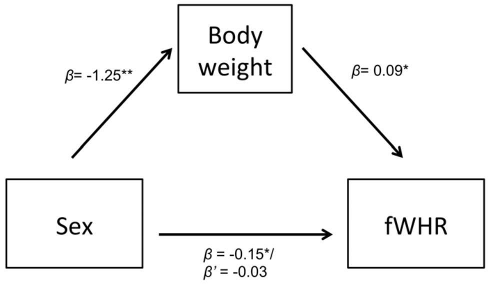


Figure 3. Mediation model of sex differences in fWHR by weight.
doi:10.1371/journal.pone.0093369.g003

the overall model, with sex and age controlled, was non-significant ($F_{3,17} = 0.39$, $p = .76$, $R^2 = .06$). Additionally, we assessed whether in adult individuals alpha status had a moderation effect on the link between fWHR and Assertiveness. A regression model with fWHR, alpha status, fWHR × alpha status, age and sex predicting Assertiveness revealed a marginal moderation effect of alpha status among adults ($\beta = 0.45$, $p = .09$).

Finally, we assessed possible influences of body weight on the relationship between Assertiveness and fWHR in the sub-sample that had weight measures available. The association of weight with Assertiveness was not significant ($r = .28$, $p = .10$), and controlling for weight using a linear regression of age, sex, weight, and fWHR on Assertiveness indicated that the relationship between Assertiveness and fWHR remained significant ($\beta = 0.58$, $p < .01$) with effects of sex ($\beta = -0.03$, $p = .88$), age ($\beta = 0.01$, $p = .98$), and weight ($\beta = -0.11$, $p = .65$) being non-significant predictors of Assertiveness.

Discussion

Our results indicated that fWHR is a sexually dimorphic trait in *Sapajus*, (although this dimorphism may be mediated by a dimorphism in body weight). In addition, *Sapajus* fWHR is closely associated with status and associated behavioural traits (i.e. assertive personality) in both adult males and adult females. This link emerged in both sexes after puberty and, unlike the evidence for sexual dimorphism, survived correction for body weight.

In capuchins, while it is possible to clearly identify and rate behavioural traits associated with dominance (e.g. aggressive wins/loses), it can be more difficult to place individuals into a precise ranking order of dominance given their relatively low rates of aggression and high levels of social tolerance compared to other primate species [32]. We therefore used Assertiveness as a measure of each monkey's relative social dominance because this measure provides a validated trait-level assessment of the behaviour of each individual across time and contexts, where each individual can be placed along a continuous gradient ranging from high to low Assertiveness. Moreover, within the Living Links population, individual differences in social status (determined by calculating David's scores using data on aggression given/received; see [41]) positively associated with scores on Assertiveness up to one year later. As such, our results support a specific link between facial structure and personality traits related to dominant behaviour in capuchins, irrespective of the group-level ranking of individuals. Nonetheless, future research assessing other measures of status or dominant behaviour will be valuable in order to establish cross species comparable links between behaviour and appearance. In particular, in the current study we did not use direct quantitative measures of dominance, which may limit the conclusions that can be drawn from the current data.

The relationship between alpha status/Assertiveness and fWHR in both sexes runs contrary to reports in humans where the link

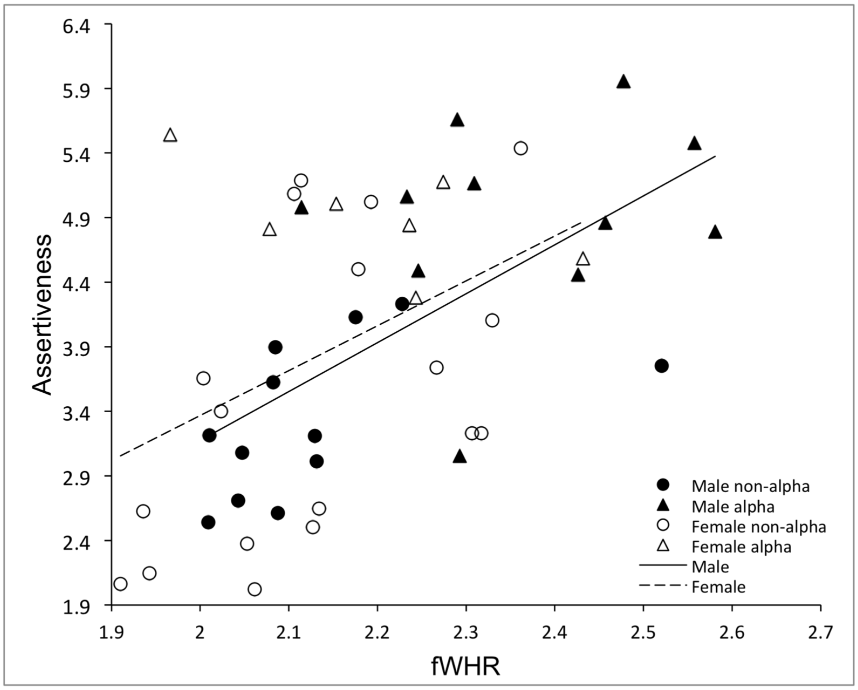


Figure 4. Association of Assertiveness and fWHR in adult males and females, split by alpha status. In both sexes a significant positive linear relationship between fWHR and Assertiveness is visible. This relationship held when examining non-alpha individuals only.
doi:10.1371/journal.pone.0093369.g004

between dominant behaviour and fWHR has been found exclusively among males (e.g. [8,10,12]). One explanation for this discrepancy might be that human and *Sapajus* females show different behaviours associated with dominance. For example, while numerous studies in humans indicate that men exhibit dominant behaviour and aggression to a much larger extent than women (e.g. [44,45]), in *Sapajus*, females are commonly observed to aggress against other females and even males, indicating perhaps that hierarchies are less sexually differentiated in *Sapajus* than in some other primate species (e.g. baboons, macaques) [32]. Thus, unlike humans, both male and female *Sapajus* may be exposed to similar selection pressures associated with dominant behaviour. While it is conceivable that the associations between face shape and behaviours linked to dominance in females reported here are specific to brown capuchins, further comparative work is necessary to test for such face-behaviour associations in a range of other primate species with varying levels of social dominance (e.g. despotic versus egalitarian species).

Weston et al. [7] previously detected sex differences in *Sapajus* fWHR using measurements taken from skulls. Here, we confirm that these sex differences exist in *Sapajus* fWHR using surface-based measurements. Importantly, this dimorphism was mediated by sex differences in body weight in the sub-sample that had weight measurements available, indicating a lack of sexual dimorphism in fWHR when size correlates are controlled, which reflects findings in humans (e.g. [20]). These results thus confirm the importance of controlling for body size when examining fWHR. To better understand the underlying mechanism(s) that link fWHR to dominant behaviour in *Sapajus* and other species, it would be of particular value to examine the sex-specificity of the behavioural correlates of fWHR (e.g. aggression), and associated endocrine profiles.

The association between fWHR and age was not significant within female *Sapajus*, suggesting that fWHR remains relatively stable throughout a female's life span; however, additional larger studies would be valuable to confirm this finding. In contrast, male fWHR was positively associated with age, suggesting an increase during sexual maturation, with adult males having a significantly larger fWHR compared to adult females and to juveniles of both sexes. These findings may indicate that male sex hormones (such as testosterone) are involved in the development of fWHR [25].

To examine the evolution of fWHR and canine size as cues to dominance linked behaviours in primates, it will be necessary to measure the association between these physical traits and behaviours associated with dominance related traits in other primate species. The lack of a significant sex difference in human fWHR [14,19,20] and canine size [21] suggests that canine size – previously argued to account for lower fWHR dimorphism in species such as *Gorilla* [7] – cannot fully account for species differences in fWHR-dimorphism. In other words, fWHR is not an obligate substitute for canine dimorphism.

Our results indicate that the same facial features are linked to competitive behaviour across different species. Indeed, humans and *Sapajus* last shared a common ancestor about 43 million years ago [46]. Thus, the existence of an association between fWHR and dominance associated behaviours in both species suggests that the relationship is phylogenetically old, perhaps derived through common selective pressures associated with dominance. However, as we have noted, further data are needed on species that vary in their display of dominance (e.g. egalitarian versus despotic species) and sexual dimorphism in order to fully understand commonality of selection pressures and behaviours.

While it is currently unclear whether facial width provides an anatomical advantage over and above mere cueing of dominance linked behaviours, at least two possibilities deserve mentioning. First, fWHR may be linked to bite strength or, in other words, superior weaponry. The masseter muscle, responsible for bite force, runs below the zygomatic arch. Thus, larger muscles that afford greater bite strength may require the zygomatic arch to be positioned more laterally, hence a greater facial width. In this case, fWHR could be a cue to bite strength, which is a marker related to dominance in several species (e.g. [47]). Second, fWHR may indicate a robust skull structure. In humans, males have stronger skulls than females, perhaps to resist fracture from blows typically encountered during fights [48]. Within males, a wider zygomatic arch may relate to a stronger skull structure, thus indicating greater ability to withstand injury during fighting encounters. Future work testing these predictions would be valuable to the understanding of relationships between fWHR and behaviours linked to dominance across species. Irrespective of possible anatomical advantages however, the current data suggest that intra-sexual selection through status competition and fighting has likely shaped the primate face.

In summary, this study demonstrates an association between facial shape and dominance related behaviour in a nonhuman species. These findings suggest a phylogenetically old link between facial structures and behaviour and underline the likely importance of such links. Further research will be needed to determine whether fWHR is used by *Sapajus* as a cue for dominance linked behaviours, particularly when encountering unfamiliar individuals (e.g. dispersing males or neighbouring groups), and whether this trait is associated with advantages to the bearer (e.g. frequency and level of aggression received from others).

Supporting Information

Data S1 Raw data presented in this manuscript.
(XLSX)

Acknowledgments

We thank all of the raters and everyone else involved in the personality study, especially Alexander Weiss, Phyllis Lee, Bernard Thierry, and Hannah Buchanan-Smith. We thank Phyllis Lee for insightful comments on this manuscript. We are grateful to Andrew Whiten and Nicolas Claidiere for permissions and assistance collecting photos at Living Links. Finally, we would like to thank Mark Bowler for providing photos of the Living Links capuchins and Catherine Talbot for providing photos of the Language Research Center capuchins

Author Contributions

Conceived and designed the experiments: CEL VADW FBM TCB. Performed the experiments: CEL VADW FBM TCB. Analyzed the data: CEL VADW TCB. Contributed reagents/materials/analysis tools: VADW TCB SFB AP. Wrote the paper: CEL VADW FBM SFB AP TCB.

References

1. Fashing PJ (2001) Male and female strategies during intergroup encounters in guerezas (Colobus guereza): evidence for resource defense mediated through males and a comparison with other primates. Behav Ecol Sociobiol 50: 219–230.
2. Plavcan JM, van Schaik CP, Kappeler PM (1995) Competition, coalitions and canine size in primates. J Hum Evol 28: 245–276.
3. Plavcan JM (2012) Sexual Size Dimorphism, Canine Dimorphism, and Male-Male Competition in Primates. Hum Nat 23: 45–67.
4. Plavcan JM, van Schaik CP (1997) Intrasexual competition and body weight dimorphism in Anthropoid primates. Am J Phys Anthropol 103: 37–68.
5. Michael PH, Deutsch J, Burney J (1994) Size, dominance and copulatory success in male northern elephant seals, Mirounga angustirostris. Anim Behav 48: 6.

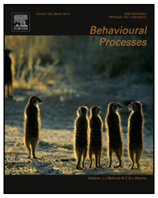
6. Alfaro JWL, Silva JS Jr, Rylands AB (2012) How different are robust and gracile capuchin monkeys? An argument for the use of Sapajus and Cebus. Am J Primatol 74: 273–286.
7. Weston EM, Friday AE, Johnstone RA, Schrenk F (2004) Wide faces or large canines? The attractive versus the aggressive primate. Proc Biol Sci 271 Suppl 6: S416–419.
8. Haselhuhn MP, Wong EM (2012) Bad to the bone: facial structure predicts unethical behaviour. Proc Biol Sci 279: 571–576.
9. Lewis GJ, Lefevre CE, Bates TC (2012) Facial width-to-height ratio predicts achievement drive in US presidents. Pers Indiv Differ 52: 855–857.
10. Stirrat M, Perrett DI (2010) Valid facial cues to cooperation and trust: Male facial width and trustworthiness. Psychol Sci 21: 349–354.
11. Stirrat M, Perrett DI (2012) Face Structure Predicts Cooperation: Men With Wider Faces Are More Generous to Their In-Group When Out-Group Competition Is Salient. Psychol Sci. 23: 718–722.
12. Carré JM, McCormick CM (2008) In your face: facial metrics predict aggressive behaviour in the laboratory and in varsity and professional hockey players. Proc Biol Sci 275: 2651–2656.
13. Deaner RO, Goetz SMM, Shattuck K, Schnotala T (2012) Body weight, not facial width-to-height ratio, predicts aggression in pro hockey players. J Res Pers 46: 235–238.
14. Özener B (2012) Facial width-to-height ratio in a Turkish population is not sexually dimorphic and is unrelated to aggressive behavior. Evol Hum Behav 33: 169–173.
15. Carré JM, McCormick CM, Mondloch CJ (2009) Facial structure is a reliable cue of aggressive behavior. Psychol Sci 20: 1194–1198.
16. Carré JM, Morrissey MD, Mondloch CJ, McCormick CM (2010) Estimating aggression from emotionally neutral faces: which facial cues are diagnostic? Perception 39: 356.
17. Masterson TJ (1997) Sexual dimorphism and interspecific cranial form in two capuchin species: Cebus albifrons and C. apella. Am J Phys Anthropol 104: 487–511.
18. Weston EM, Friday AE, Lio P (2007) Biometric Evidence that Sexual Selection Has Shaped the Hominin Face. PLoS One 2: e710.
19. Kramer RS, Jones AL, Ward R (2012) A Lack of Sexual Dimorphism in Width-to-Height Ratio in White European Faces Using 2D Photographs, 3D Scans, and Anthropometry. PLoS One 7: e42705.
20. Lefevre CE, Lewis GJ, Bates TC, Dzhelyova M, Coetzee V et al. (2012) No evidence for sexual dimorphism of facial width-to-height ratio in four large adult samples. Evol Hum Behav 33: 623–627.
21. Kapila R, Nagesh KS, Ivengar AR, Mehkri S (2011) Sexual Dimorphism in Human Mandibular Canines: A Radiomorphometric Study in South Indian Population. J Dent Res Dent Clin Dent Prospects 5: 51–54.
22. Mazur A, Booth A (1998) Testosterone and dominance in men. Behav Brain Sci 21: 353-363.
23. Bercu BB, Lee BC, Pineda JL, Spiliotis BE, Denman DW et al. (1983) Male sexual development in the monkey. I. Cross-sectional analysis of pulsatile hypothalamic-pituitary-testicular function. J Clin Endocrinol Metab 56: 1214–1226.
24. Rey R, Campo S, Ayuso S, Nagle C, Chemes H (1995) Testicular steroidogenesis in the Cebus monkey throughout postnatal development. Biol Reprod 52: 997–1002.
25. Lefevre CE, Lewis GJ, Perrett DI, Penke L (2013) Telling facial metrics: facial width is associated with testosterone levels in men. Evol Hum Behav 34: 273–279.
26. Izawa K (1980) Social Behavior of the Wild Black-capped Capuchin (Cebus apella). Primates 21: 443–467.
27. Janson C (1985) Aggressive competition and individual food consumption in wild brown capuchin monkeys (Cebus apella). Behav Ecol Sociobiol 18: 125–138.
28. Boinski S (1996) Vocal communication of troop movement in squirrel monkeys (Saimiri oersetdi and S. sciureus) and white faced capuchins (Cebus capucinus). In M.A. Norconk, A.L. Rosenberger & P.A. Garber (Eds.), Adaptive radiations of neotropical primates 251–268. Springer.
29. Di Bitetti MS (1997) Evidence for an important social role of allogrooming in a platyrrhine primate. Anim Behav 54: 199–211.
30. Wheeler BC, Scarry CJ, Koenig A (2013) Rates of agonism among female primates: a cross-taxon perspective. Behavioral Ecology 24: 1369–1380.
31. de Waal FBM (1984) Sex differences in the formation of coalitions among chimpanzees. Ethology & Sociobiology 5: 239–255.
32. Fragaszy DM, Visalberghi E, Fedigan LM (2004) The Complete Capuchin. Cambridge University Press.
33. Morton FB, Lee PC, Buchanan-Smith HM, Brosnan S, Thierry B et al. (2013) Personality structure in brown capuchin monkeys: comparisons with chimpanzees, orangutans, and rhesus macaques. J Comp Psychol 127: 282–298.
34. Coetzee V, Chen J, Perrett DI, Stephen ID (2010) Deciphering faces: Quantifiable visual cues to weight. Perception 39: 51–61.
35. ASAB (2012) Guidelines for the treatment of animals in behavioural research and teaching. Anim Behav 83: 301–309.
36. National Centre for the Replacement Refinement & Reduction of Animals in Research. (2006) NC3Rs Guidelines: Primate accommodation, care and use. London: National Centre for the Replacement, Refinement & Reduction of Animals in Research.
37. Macdonald C, Whiten A (2011) The 'Living Links to Human Evolution' Research Centre in Edinburgh Zoo: A new endeavour in collaboration. International Zoo Yearbook 45: 7–17.
38. Leonardi R, Buchanan-Smith HM, Dufour V, MacDonald C, Whiten A (2010) Living together: behavior and welfare in single and mixed species groups of capuchin (Cebus apella) and squirrel monkeys (Saimiri sciureus). Am J Primatol 72: 33–47.
39. Tiddeman BP, Perrett DI, Burt DM (2001) Prototyping and transforming facial textures for perception research. IEEE Comput Graph Appl 21: 42–50.
40. Weiss A, Inoue-Murayam M, Hong KW, Inoue E, Udono T, et al. (2009) Assessing chimpanzee personality and subjective well-being in japan. Am J Primatol 71: 283–292.
41. Gammell MP, de Vries H, Jennings DJ, Carlin CM, Hayden TJ (2003) David's score: a more appropriate dominance ranking method than Clutton-Brock et al.'s index. Animal behaviour 66: 601–605.
42. R Core Team (2012). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
43. Preacher KJ, Hayes AF (2008) Asymptotic and resampling strategies for assessing and comparing indirect effects in multiple mediator models. Behav Res Methods 40: 879–891.
44. Archer J (2004) Sex differences in aggression in real-world settings: A meta-analytic review. Rev Gen Psychol 4: 291−322.
45. Archer J (2009) Does sexual selection explain human sex differences in aggression? Behav Brain Sci 32: 249−266.
46. Steiper ME, Young NM (2006) Primate molecular divergence dates. Mol Phylogenet Evol 41: 384–394.
47. Clutton-Brock TH (1983) Selection in relation to sex. In B. J. Bendall (Ed.), Evolution from Molecules to Men, 457–481, Cambridge: Cambridge University Press.
48. Buikstra J, Ubelaker D (1994) Standards for data collection from human skeletal remains: proceedings of a seminar at the field museum of natural history. Arkansas Archeological Survey Research Series No. 44, Fayetteville, AR.

Behavioural Processes 124 (2016) 38–46

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc



Using photographs to study animal social cognition and behaviour: Do capuchins' responses to photos reflect reality?

F. Blake Morton[a,b,*], Sarah F. Brosnan[c], Laurent Prétôt[c], Hannah M. Buchanan-Smith[a,b], Eoin O'Sullivan[a,b], Martina Stocker[d], Daniel D'Mello[a], Vanessa A.D. Wilson[b,e]

[a] *Behaviour and Evolution Research Group, Psychology, School of Natural Sciences, University of Stirling, UK*
[b] *Scottish Primate Research Group, UK*
[c] *Department of Psychology and Language Research Center, Georgia State University, GA, USA*
[d] *Department of Cognitive Biology, University of Vienna, Austria*
[e] *Department of Psychology, University of Edinburgh, UK*

ARTICLE INFO

Article history:
Received 21 April 2015
Received in revised form 30 August 2015
Accepted 9 October 2015
Available online 22 October 2015

Keywords:
Brown capuchin monkey
Sapajus apella
Ecological validity
Image
Social decision-making
Visual media
Visual perception

ABSTRACT

Behavioural responses to photos are often used to infer what animals understand about their social environment, but are rarely validated against the same stimuli in real life. If subjects' responses to photos do not reflect responses to the same live stimuli, it is difficult to conclude what happens in reality based on photo responses alone. We compared capuchins' responses to photos versus live stimuli in an identical scenario within research cubicles. Subjects had the opportunity to approach food placed in front of an alpha group member and, in a separate condition, photos depicting the same individual. Subjects' latencies to approach food when placed in front of the real alpha negatively correlated with time subjects spent in close proximity to the alpha in their main enclosure. We therefore predicted subjects' latencies to approach food in the presence of photos would positively correlate with their latencies to approach food in the presence of the real alpha inside the cubicles, but negatively correlate with time they spent in proximity to the alpha in their enclosure. Neither prediction was supported. While not necessarily surprising, we explain why these results should be an important reminder that care is needed when interpreting results from photo studies.

1. Introduction

Visual media are widely used to study animal social cognition and behaviour, particularly how animals perceive, understand, and respond to social information (Bovet and Vauclair, 2000; Fagot and Parron, 2010; Fagot et al., 2010). For instance, researchers may record subjects' responses to photos or videos depicting social situations (e.g. the face of a familiar group member, or the perinea of a sexually receptive female; Bovet and Vauclair, 2000; Schell et al., 2011). Photos are particularly favoured among researchers because they are easier than videos to manipulate and control for specific variables (e.g. colour saturation, size/shape; Rowland and Perrett, 1995), can be manipulated in a realistic fashion (e.g. placing photos in a location where the real animal might be found), and allow researchers to explore subjects' responses to individuals or situations that would otherwise be difficult or impossible to recreate naturally.

Throughout the literature, animals' responses to photos, such as their spontaneous reactions (e.g. facial expressions, eye gaze) or their ability to discriminate and categorise social content (e.g. familiar versus unfamiliar, kin versus non-kin), have been used to explore animals' reactions to social stimuli in controlled ways (reviewed in Bovet and Vauclair, 2000). These data are often interpreted as being socially meaningful. For example, baboons (*Papio hamadryas*) gaze longer at images of conspecifics' eyes compared to images of their mouths and noses, suggesting that the eyes are the most salient feature of faces for this species (Kyes and Candland, 1987). European starlings (*Sturnus vulgaris*) and domesticated sheep (*Ovis aries*) respond less fearfully and more affiliatively to images of conspecifics compared to controls (e.g. photos of humans and landscapes), suggesting that they process and are attracted to the social content of those images (Vandenheede and Bouissou 1994, 1995; Perret et al., 2015). Finally, dogs are able to discriminate between photos of happy versus angry faces of

---

[*] Corresponding author at: Psychology, School of Natural Sciences, University of Stirling, Stirling FK9 4LA, UK.
E-mail address: Morton.blake@gmail.com (F.B. Morton).

http://dx.doi.org/10.1016/j.beproc.2015.10.005
0376-6357/

humans, suggesting that they are sensitive to humans' emotional states (Müller et al., 2015).

In many of these cases, we can learn quite a lot from photos. For instance, if an animal discriminates from photos certain individuals better than others (e.g. known versus unknown individuals), or focuses on a particular feature of photos (e.g. the eyes), it can help researchers identify what aspects of those stimuli are most salient to the animal. Although we still may not know how the animal interpreted the photos, the fact that they can, for instance, discriminate a photo of a known individual better than that of a stranger at least tells us that they better recognize familiar individuals. Even if they are using non-social cues (e.g. colour preference; D'Amato and Van Sant, 1988), it may be that they are also using the same cues in real life to make those discriminations.

Nevertheless, using photos to specifically understand social cognition and behaviour based on responses to photos alone is challenging. If subjects do not react to an image as they would a real animal, then the results do not necessarily tell us anything about what happens in reality. As such, results can be more ambiguous without comparing subjects' responses to the same live stimuli as a baseline. For example, in cases of spontaneous reactions to photos, a male subject may be curious or confused about a "frozen" image of a female conspecific, and therefore spend more time exploring or gazing at that image; yet, the same response could also be interpreted as a sign of sexual attraction—as is often the case in studies of primates (e.g. Griffey, 2011; Pflüger et al., 2014; Waitt et al., 2003; Waitt and Little, 2006). Given the absence of other sensory cues (noise, smell, movement), there also remains the possibility that subjects treat social content in photos as inanimate features of "objects" rather than depictions of socially-relevant stimuli, which, under certain experimental paradigms (e.g. where spontaneous reactions are recorded), might affect an animal's decision-making on the task, or their motivation to attend to certain features of the stimuli. Therefore, establishing whether subjects' responses to photos reflect their responses to the same stimuli in real life can help researchers address these concerns.

Researchers very rarely compare animals' responses to photos to the same stimuli in real life. For some experimental paradigms, e.g. in cases where photos are digitally manipulated, this may not be feasible. However, when it is possible to do so, such a comparison may be a useful tool for interpreting the social relevance of subjects' responses to photos, particularly where the assumption is that behavioural reactions to photos are equivalent to their reactions to the same, live stimuli (e.g. testing hypotheses about mate choice preferences; Griffey, 2011; Waitt et al., 2003; Waitt and Little, 2006). If subjects respond to photos as they do towards the same live stimuli, it supports the notion that subjects treat photos as they do in reality; meaning, behavioural reactions to images may tell us something about subjects' perception and understanding of live social stimuli. If, however, subjects' responses to photos do not reflect how they respond to the same stimuli in real life, it suggests that it may not be safe to assume those responses reflect subjects' real-life social behaviour and/or socio-cognitive skills. In such instances, results must be interpreted with caution. For studies that require the use of images, it may be beneficial to include more sophisticated forms of experimentation, such as fMRI analyses to identify neural mechanisms, to help interpret the data.

We tested whether brown capuchin monkeys (*Sapajus* sp., formerly *Cebus apella*; Alfaro et al., 2012) would react to social stimuli (depicted in photos) as they would the same, live stimuli. Researchers often use "floating faces", i.e. an image of a face with no body, to test social perception in animals (Bovet and Vauclair, 2000; Guo et al., 2003; Pokorny and de Waal, 2009; Griffey, 2011), but full body images may provide stronger social cues and are the only direct comparison to a real animal. We therefore gave our subjects the opportunity to approach or avoid food placed in front of either a floating face (i.e. a cut-out colour photo of a face without a body) or a full body image (i.e. life-size, cut-out colour photo) of an alpha member of their own group. Most studies utilizing images rely on a computerized presentation in which the images depict animals in locations that real animals never inhabit (e.g. on a computer screen outside the animal's enclosure). This makes a direct comparison between photos and real stimuli impossible. Therefore, in the current study, we presented cut-out printed images of the alpha to subjects within research cubicles, which enabled us to test subjects individually under controlled conditions, but in a location where they were accustomed to seeing real conspecifics (i.e. other members of their group). Subjects' responses to the images were then compared to their latencies to approach food when the real alpha (the same individual depicted in photos) was inside an adjacent cubicle, and the total amount of time subjects spent in close proximity to the real alpha within their group's main indoor/outdoor enclosure (i.e. a natural, non-experimental context). Wild and captive studies of brown capuchins have shown that relatively lower-ranking individuals often avoid close proximity to higher-ranking group members, presumably to avoid aggression (e.g. Fragaszy et al., 2004; Janson, 1990; Morton, 2014). We therefore predicted that subjects' latencies to approach food in the presence of photos would be positively related to their latencies to approach food when the real alpha was inside the cubicles. We also predicted that subjects' responses to photos within the cubicles would be negatively related to the amount of time they spent in close proximity to the real alpha in their main enclosure.

2. Methods and materials

2.1. Study sites and subjects

There were eighteen subjects from two sites. Five juveniles (between 1 and 4 years old; Fragaszy et al., 2004) and six adults (>4 years old) were housed at the "Living Links to Human Evolution" Research Center (LL), UK (Leonardi et al., 2010; MacDonald and Whiten, 2011). Age of these study subjects ranged from 2.29 to 8.17 years for males (average 4.81 ± SD 2.01 years, $N = 8$ capuchins), and 5.63 to 13.28 years for females (average 9.68 ± SD 3.85 years, $N = 3$ capuchins). The other seven monkeys were adults, and housed at the Language Research Center (LRC) of Georgia State University, USA. Age of these study subjects ranged from 7 to 11 years for males (average 9.3 ± SD 2.08 years, $N = 3$ capuchins), and 12 to 18 years for females (average 15.25 ± SD 3.2 years, $N = 4$ capuchins). Further details on group composition and animal husbandry at each site are provided in Section 2.1 of the Supplementary electronic materials.

2.1.1. Subjects' prior experience with photos

At LL, four adults participated in a study by Griffey (2011), which took place in 2010 and involved presenting subjects with photos of the faces of unfamiliar capuchins. One of these adults (Kato) was also the subject of an eye-tracking study in November, 2012, whereby he was exposed to photos of unfamiliar and familiar group members (Living Links, unpub. data). At the LRC, all subjects had prior experience with a facial discrimination study using photos of the faces of familiar and unfamiliar conspecifics, which took place between February and November, 2013 (one female was still participating in the facial discrimination study at the time of testing for this study). All of the previous studies at both sites displayed photos on computer screens (i.e. pixelated glowing images) and photos were not to scale. Subjects had never before seen printed photos of conspecifics nor full body photos like those used in the present study (Section 2.3). Subjects also had never before been exposed to photos placed inside the research cubicles where testing for this study took place.

Table 1
Summary of each experimental photo condition administered to the Living Links (LL) and Language Research Center (LRC) monkeys.

Experimental condition	Description	Study location
Face-Direct	Floating face with direct eye gaze	LL
Full Body-Direct	Full body with direct eye gaze	LL
Face-Averted	Floating face with averted eye gaze	LL and LRC
Full Body-Averted	Full body with averted eye gaze	LL and LRC
Real Monkey	Real monkey in adjacent cubicle	LL

2.1.2. *Ethical standards*

Subjects' participation in this study was entirely voluntary; they were able to access the research cubicles via a corridor connecting the cubicles to their main enclosure. This study was approved by Living Links, the IACUC of Georgia State University, and complied with regulations of the Association for the Study of Animal Behaviour (ASAB, 2012).

2.2. *Photos of monkeys*

Subjects were presented with photos of an alpha monkey from their group. Alpha status was determined based on behavioural observations including wariness of other group members, how much aggression individuals received, how many fights individuals won versus lost, whether they were being sought out for mating, how many offspring they sired/gave birth to, their level of assertive behaviour (e.g. manipulative, bold, aggressive) relative to others, how often they received and gave grooming to others, and their ability to take food from humans and other monkeys (see Fragaszy et al., 2004; Lefevre et al., 2014; Morton et al., 2013; Morton, 2014). The combination of these traits allow for easy and straight-forward recognition of alpha status among our capuchins. Lefevre et al. (2014) reported complete inter-rater agreement for alpha status assignment for the monkeys used in our study, using raters with at least one year of experience working with the monkeys from their site.

All photos were taken within six months prior to testing, and depicted each monkey's face angled towards the camera (Section 2.2 in the Supplementary electronic materials). The Face-Direct and Full Body-Direct conditions used photos depicting the alpha monkey's eyes gazing into the camera, while the Face-Averted and Full Body-Averted conditions used photos depicting an averted gaze (Table 1; Section 2.3). Within each group of monkeys, the same test subjects were all exposed to photos of the same alpha individual. Photos were printed in colour on xerox paper to reduce glare from light and mounted on stiff cardboard to avoid bending during the study. All photos were life-size, which was estimated visually while the monkeys were inside the research cubicles.

2.3. *Experimental conditions*

There were five experimental conditions (Table 1). At LL, the Face-Direct and Full Body-Direct conditions preceded the Face-Averted and Full Body-Averted conditions. Therefore, the Face-Averted and Full Body-Averted conditions were replicated at the LRC to address the possibility that the LL monkeys' responses to these conditions were affected by their recent exposure to the Face-Direct and Full Body-Direct conditions (e.g. habituation to photos). The LRC subjects did not undergo the Face-Direct and Full Body-Direct conditions since the sole purpose of their involvement was to replicate the Face-Averted and Full Body-Averted conditions among a sample of capuchins that was naïve to the study.

The Face-Direct and Face-Averted conditions tested capuchins' responses to photos depicting a “floating face”; that is, a life-size colour image of the alpha's face with no body, displayed on a plain piece of white 21 × 29.7 cm paper (Fig. 1a). At LL, the photo and paper was always taped to the far end of cubicle B at the capuchins' eye level. At the LRC, the photo and paper was attached to a wooden stand located 5 cm from the far end of cubicle B, in the same location as stimuli used in training and to administer the Full Body-Averted condition.

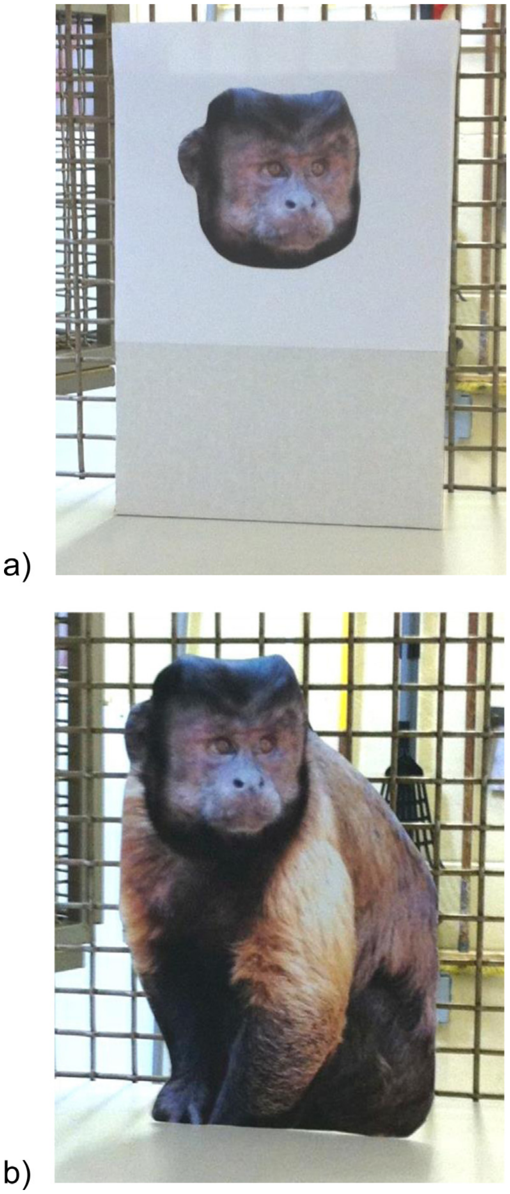


Fig. 1. Example of (a) a floating face glued to a white sheet of paper and (b) a full body photo from the LRC.

The Full Body-Direct and Full Body-Averted conditions tested subjects' responses to photos of the same alpha monkey shown to them in the other photo conditions, but depicting a full body image; that is, a life-size, cut-out colour image of the individual, with full body and no background (Fig. 1b). The cut-out photo was glued to cardboard using non-scented glue, and placed upright on a small wooden stand (not visible to the subject) inside the test cubicle to give the impression that the monkey was sitting inside the cubicle. The photo was approximately 5 cm behind the food reward.

2.4. *Setup*

Training and testing took place inside research cubicles. Each subject was tested individually. All training/testing trials lasted for

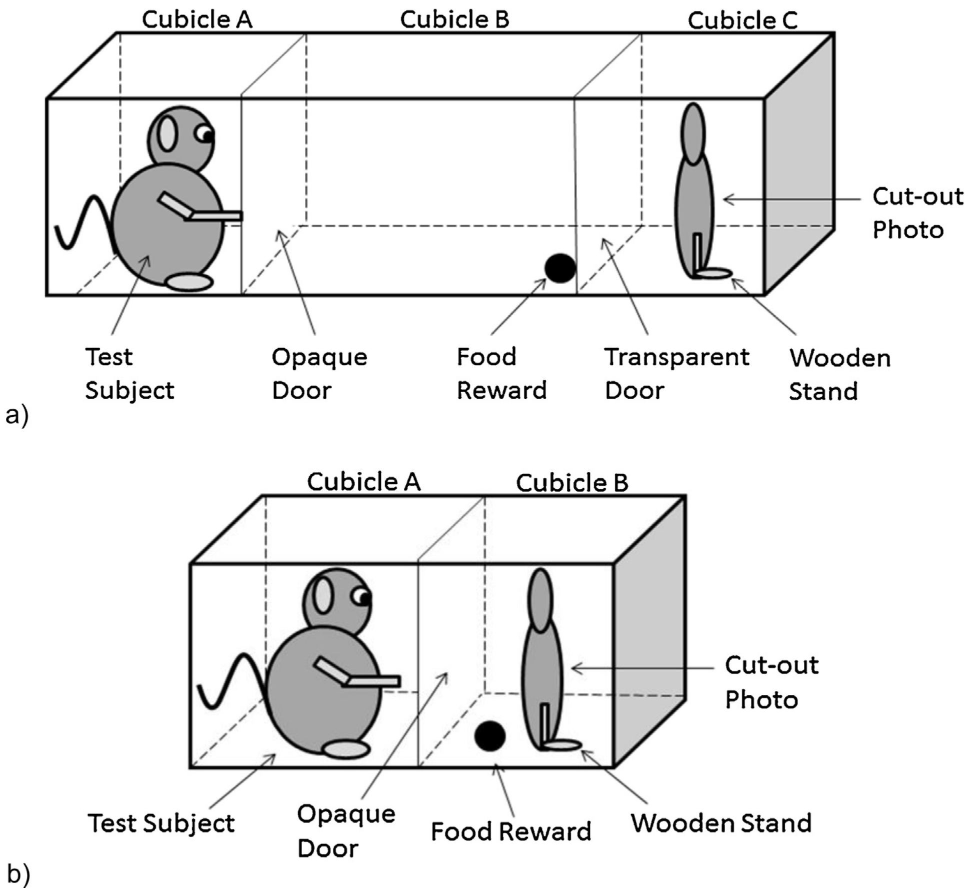


Fig. 2. Illustration of the experimental setup involving a full body photo administered to monkeys at (a) Living Links and (b) the Language Research Center.

one minute (or up to five minutes at the LRC), or until subjects made physical contact with the food reward. At no point during this study did any subject end testing prematurely (e.g. by gesturing to the cubicle door exit).

Fig. 2a depicts the general setup at LL. The heights and widths of cubicles A–C were exactly the same (52.1 cm × 51.4 cm); however, the middle cubicle (cubicle B) was twice the length of cubicles A and C (cubicle B: 99 cm; cubicle A/C: 49.5 cm). An opaque Plexiglas sliding door separated cubicles A and B, while a transparent sliding door separated cubicles B and C. During training and experimental trials, a subject was closed inside cubicle A. Then, a researcher would open the opaque door leading into cubicle B, which contained a highly-preferred food reward—a cluster of approximately six raisins.

Fig. 2b depicts the general setup at the LRC. Cubicles A and B had the same dimensions (71.12 cm in width × 71.12 cm in length × 60.96 cm in height), and were separated by an opaque Plexiglas sliding door. Similar to the LL setup, during training and experimental trials the LRC subjects were closed inside cubicle A. Then, a researcher would open the opaque door leading into cubicle B, which contained a highly preferred food reward (i.e. one full small grape or half a big grape).

At both sites, care was taken to ensure that subjects were paying attention and standing at the door leading into cubicle B, i.e. waiting to enter the cubicle, before the researcher opened it. During all training and experimental trials, subjects were allowed to enter cubicle B and freely take the food reward. No other food was given to the subject until the end of the trial. All non-participating subjects were kept out of the testing area so they would not have any exposure to the setup prior to their own test.

2.5. *Training*

2.5.1. *Living Links*

Training at LL took place between 30 September and 14 October, 2013. In preliminary runs, it was estimated that it would take subjects approximately 2–3 s to walk (at a normal pace) from cubicle A to cubicle C. Therefore, subjects underwent at least one training trial per day until their minimum latency to obtain food rewards was approximately 3 s for three consecutive trials. In all trials, a plain sheet of white paper (21 cm × 29.7 cm) was taped to the middle of the door of cubicle B and C, on the cubicle C side. Food rewards were placed on the floor of cubicle B, approximately 5 cm in front of the paper. The purpose of the white paper was to habituate subjects to the presence of a “foreign object” within the cubicles prior to tests involving floating face images, which also had a white background (Section 2.3; Fig. 1a).

2.5.2. *Language Research Center*

Training at the LRC took place between 5 and 12 April, 2014, and was similar to the LL setup (Fig. 2b). In preliminary runs, it was estimated that it would take subjects approximately 2 s to walk (at a normal pace) from cubicle A to cubicle B. The shorter times here were due to the smaller size of the testing area compared to those at LL. Subjects underwent at least one training trial per day until their minimum latency to obtain food rewards remained approximately 2 s for three consecutive trials. As at LL, training was done with a white piece of paper in the same location as the photos used for testing; the paper was mounted on a wooden stand located approximately 5 cm from the far side of the testing chamber.

2.6. Testing

Subjects underwent each experimental condition only once. At LL, testing took place between 8 and 28 October, 2013. Conditions were counterbalanced across testing days such that no more than half the subjects received the same condition on the same day, and each monkey underwent no more than two conditions on the same day.

At the LRC, testing took place between 14 and 15 April, 2014. Conditions were counterbalanced and subjects were tested only once per day on each condition.

2.7. Measuring latencies to take food rewards

Sessions were video recorded at both sites; latencies were also recorded in real time. To test for inter-observer reliabilities, an independent observer coded 25% of the video data from each site, and these codings were compared to the latency measurements recorded in real time for the same exact trials. “Latency to obtain food” was defined as the time in seconds it took for the subject to make physical contact with the food reward (e.g. touch with mouth or hand) after the door separating cubicles A and B began to slide open. In all trials, the experimenter opened the door in approximately 1 s. Subjects’ latencies during their last trial of training were used as a “control” condition (i.e. after subjects were fully trained, but before any experimental stimuli were presented) to compare to subjects’ responses to each experimental condition; the control condition would indicate whether subjects were reacting to each photo stimulus.

2.8. Measuring behaviour towards the real alpha monkey

Using scan sampling methods (Martin and Bateson, 2007), spatial proximity data were recorded at each site within each group’s main indoor/outdoor enclosure approximately six weeks prior to the start of subjects’ training. At LL, behavioural observations were made between 9 and 18 h from 23 August to 3 October, 2013, with three samples taken each day. At the LRC, behavioural observations were made between 8:30 and 9 h from 28 January to 10 March, 2014, and samples were recorded every three minutes over 30 min, for a total of 11 samples each week. Any monkey located within one body length of the sampled individual was identified and noted. At LL, a total of 92 scans were collected for the East group, and 89 for the West group. At the LRC, a total of 110 scans were collected for Griffin’s group and 88 scans were collected for Gabe’s group. All monkeys were sampled equally at both sites. Individual scores were calculated for each monkey by summing the total number of samples in which subjects spent in close proximity to the alpha monkey depicted in the photos.

2.8.1. Validation of the spatial proximity measures

To establish whether spatial proximity was a relevant behaviour to compare with subjects’ latencies in conditions involving photos, monkeys at LL underwent a single trial (Real Monkey condition; Table 1) during which they were required to obtain food when the real alpha monkey was sitting inside cubicle C. Testing took place between 11 and 21 October, 2013, and was counter balanced with the Face-Direct and Full Body-Direct conditions.

2.9. Statistical analyses

Pearson correlations were used to test for inter-observer reliabilities in measuring subjects’ latencies to approach food. Correlation coefficients $r > 0.9$ were defined as high inter-observer reliability.

Bootstrapped *t*-tests were used to test for significant differences in subjects’ latencies to approach food between training and experimental conditions (Table 1). To reduce the risk of capitalizing on Type 1 error inflation due to our multiple comparisons, we also ran one-way ANOVA tests between conditions using a post hoc Bonferroni correction.

To investigate possible age-related differences in photo perception (e.g. Schell et al., 2011), bootstrapped Pearson correlations were used to test for significant associations between age (in years) and subjects’ latencies to approach food in each photo condition. Bonferroni corrections were applied to significant results. Age-related analyses were only necessary for the LL subjects since the LRC subjects were all adults.

Bootstrapped Pearson correlations were used to test associations between subjects’ latencies to obtain food in all photo conditions and the Real Monkey condition, and between photo conditions and the amount of time subjects spent in close proximity to the real alpha in their main enclosure. Bonferroni corrections were applied to significant results. Significant differences between the *r*-values for conditions involving full body and floating face images were determined using Fisher’s *z*-tests.

Fisher’s *z*-tests were conducted in R (version 3.0.1). All other analyses were conducted using SPSS 21.0 (SPSS, IBM Corp., Chicago, USA). Analyses involving each photo condition were conducted with and without including monkeys with prior photo experience (Section 2.1). For all bootstrapped analyses, 95% confidence intervals (CI) were generated (with replacement = 10,000) using the bias-corrected and accelerated bootstrap (Efron 1987; Davison and Hinkley, 1997).

3. Results

3.1. Inter-observer reliability tests

Latency measurements were highly concordant between the blind observer and the researchers who coded the video data (LL video: $r = 0.98$, $P < 0.001$, $N = 20$ trials; LRC video: $r = 0.99$, $P < 0.001$, $N = 14$ trials). Thus, latency measurements were considered reliable at both sites.

3.2. Validation of the spatial proximity measures

Subjects’ latencies to obtain food in the Real Monkey condition (Table 1) were negatively correlated with the amount of time they spent in close proximity to the alpha within their main enclosure ($r = -0.65$, bootstrapped 95% CI = [−0.77, −0.65], $N = 11$); meaning, subjects who spent less time in close proximity to the alpha also took longer to approach food when the alpha was inside the cubicles. Thus, the spatial proximity data were considered a behaviourally valid measure to compare with monkeys’ latencies to obtain food in the presence of each photo stimuli (Table 1).

3.3. Differences in latencies between training and experimental photo conditions

The LL subjects underwent an average of 6 ± SD 1.10 training trials in which no photo stimuli were presented. Average latency to obtain food rewards during the final trial of training was 2.18 ± SD 0.75 s. During testing with photos, subjects’ average latency to obtain food rewards was 4.50 ± SD 2.54 s in the Face-Direct condition (i.e. floating face with direct eye gaze), 9.54 ± SD 6.0 s in the Full Body-Direct condition (full body photo with direct eye gaze), 2.05 ± SD 0.91 s in the Face-Averted condition (floating face with averted gaze), 2.86 ± SD 0.89 s in the Full Body-Averted condition (full body photo with averted gaze), and 10.45 ± SD 17.11 s in the Real Monkey condition (i.e. the real alpha in an adjacent cubicle).

Table 2
Age-related effects on subjects' responses to photo stimuli.

	Pearson correlations[a]	
	r	95% CI[b]
Face-Direct condition	−0.192	[−0.751, 0.773]
Full Body-Direct condition	−0.29	[−0.77, 0.463]
Face-Averted condition	−0.063	[−0.691, 0.866]
Full Body-Averted condition	−0.128	[−0.691, 0.329]

[a] Pearson correlations between the LL subjects' ages (in years) and their responses to photo stimuli in each condition.

[b] Bias-corrected and accelerated bootstrapped 95% confidence intervals (CI).

Age did not correlate with subjects' responses to each photo condition (Table 2). Compared to subjects' final training session (i.e. the controlled condition), subjects exhibited on average significantly longer latencies to obtain food rewards in the Face-Direct condition (t = −3.14, df = 10, bootstrapped 95% CI = [−4.15, −0.59]), Full Body-Direct condition (t = −3.99, df = 10, bootstrapped 95% CI = [−11.18, −4.09]), the Real Monkey condition (t = −1.63, df = 10, boot- strapped 95% CI = [−18.64, −1.18]), the Full Body-Averted condition (t = −2.68, df = 10, bootstrapped 95% CI = [−1.18, −0.23]), but not in the Face-Averted condition (t = 0.38, df = 10, bootstrapped 95% CI = [−0.68, 0.86]). Mean latencies in the Face-Direct condition were significantly shorter than those in the Full Body-Direct condition (t = −2.57, df = 10, bootstrapped 95% CI = [−9.70, −1.64]), but significantly longer compared to the Face-Averted condition (t = 3.75, df = 10, bootstrapped 95% CI = [1.41, 3.82]) and the Full Body-Averted condition (t = 2.41, df = 10, bootstrapped 95% CI = [0.55, 3.09]). Latencies in the Face-Direct condition were significantly shorter than those in the Real Monkey condition (t = −1.63, df = 10, bootstrapped 95% CI = [−19.67, −1.45]). Latencies in the Full Body-Direct condition were significantly shorter than those in the Real Monkey condition (t = −1.51, df = 10, bootstrapped 95% CI = [−19.76, −0.77]). Latencies in the Full Body-Direct condition did not significantly differ from those in the Real Monkey condition (t = −0.17, df = 20, bootstrapped 95% CI = [−15.32, 8.49]). A one-way ANOVA with Bonferroni correction revealed a significant difference in monkeys' latencies to approach food across conditions (F(5,60) = 2.80, P = 0.03). Compared to subjects' final training session, subjects exhibited on average significantly longer latencies to obtain food rewards in the Face-Direct condition (mean difference = −2.32, bootstrapped 95% CI = [−3.88, −0.83]), the Full Body-Direct condition (mean difference = −7.36, bootstrapped 95% CI = [−11.24, −3.88]), and the Real Monkey condition (mean difference = −8.27, bootstrapped 95% CI = [−21.02, −0.71]), but not in the Face-Averted condition (mean difference = 0.14, bootstrapped 95% CI = [−0.59, 0.89]) or the Full Body-Averted condition (mean difference = −0.68, bootstrapped 95% CI = [−1.36, 0.03]) (Fig. 3a). Mean latencies in the Face-Direct condition were significantly shorter compared to those in the Full Body-Direct condition (mean difference = −5.05, bootstrapped 95% CI = [−9.14, −1.55]), and significantly higher compared to the Face-Averted condition (mean difference = 2.46, bootstrapped 95% CI = [1.05, 4.02]) and the Full Body-Direct condition (mean difference = 1.64, bootstrapped 95% CI = [0.22, 3.15]). Latencies in the Face-Direct condition did not significantly differ from those in the Real Monkey condition (mean difference = −5.95, bootstrapped 95% CI = [−18.92, 1.76]). Latencies in the Full Body-Direct condition did not differ significantly from those in the Real Monkey condition (mean difference = −0.91, bootstrapped 95% CI = [−14.88, 8.31]). Latencies in the Face-Averted condition did not significantly differ from those in the Full Body-Averted condition (mean difference = 0.82, bootstrapped 95% CI = [−0.01, 1.61]).

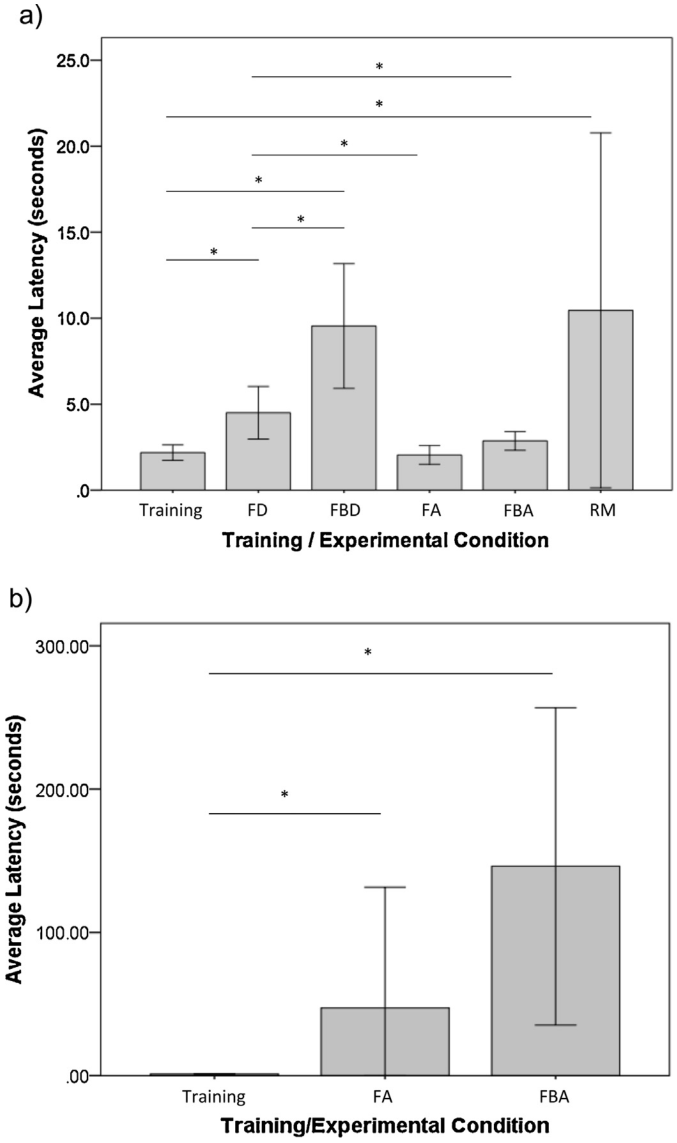


Fig. 3. Average latencies to obtain food rewards in training and experimental conditions among the (a) Living Links monkeys and (b) LRC monkeys. FD—floating face with direct eye gaze, FBD—full body photo with direct eye gaze, FA—floating face with averted eye gaze, FBA—full body with averted eye gaze. *—Statistically significant based on a 95% CI bootstrapped one-way ANOVA with Bonferroni correction. Error bars represent standard errors from the mean.

At the LRC, subjects underwent four training trials; average latency to obtain food rewards during the final trial of training was 1.09 ± SD 0.17 s. Subjects' average latency to obtain food was 47.26 ± SD 111.53 s in the Face-Averted condition, and 146.12 ± SD 146.51 s in the Full Body-Averted condition. Compared to subjects' final training session (i.e. the control condition), subjects exhibited on average significantly longer latencies to obtain food rewards in the Face-Averted condition (t = −1.10, df = 6, bootstrapped 95% CI = [−132.87, −1.08]) and the Full Body-Averted condition (t = −2.62, df = 6, bootstrapped 95% CI = [−256.81, −45.43]), respectively. Latencies in the Full Body-Averted condition were significantly longer than those in the Face-Averted condition (t = −1.89, df = 6, bootstrapped 95% CI = [−183.22, −12.83]). A one-way ANOVA with Bonferroni correction revealed a non-significant trend in differences between monkeys' latencies to approach food in each condition (F(2,18) = 3.40, P = 0.06). Compared to subjects' final training session, subjects showed significantly longer latencies to obtain food rewards in the Face-Averted condition (mean difference = −46.17, bootstrapped 95% CI = [−152.97, −1.13]) and the Full Body-Averted condition (mean difference = −145.04,

Table 3
Correlations between LL subjects' responses to each photo condition and real monkey conditions.

	Real Monkey condition[a]		Spatial proximity[b]	
	r	95% CI[c]	r	95% CI[c]
Face-Direct condition	0.173	[−0.365, 0.845]	−0.249	[−0.751, 0.756]
Full Body-Direct condition	0.149	[−0.449, 0.848]	−0.454	[−0.885, 0.418]
Face-Averted condition	0.147	[−0.532, 0.821]	−0.352	[−0.84, 0.505]
Full Body-Averted condition	0.573	[−0.01, 0.883]	−0.485	[−0.856, 0.45]

[a] Pearson correlations between the LL subjects' latencies to approach stimuli in photo conditions and their latencies in the real monkey cubicle condition.
[b] Pearson correlations between the LL subjects' latencies to approach stimuli in photo conditions and time spent in close proximity to alpha in main enclosure.
[c] Bias-corrected and accelerated bootstrapped 95% confidence intervals (CI).

bootstrapped 95% CI = [−249.95, −37.94]); however, latencies in the Face-Averted condition did not significantly differ from those in the Full Body-Averted condition (mean difference = −98.86, bootstrapped 95% CI = [−220.89, 27.67]) (Fig. 3b).

3.4. *Responses to photos versus real monkeys*

At LL, subjects' latencies in photo conditions were not significantly related to their latencies to approach food in the Real Monkey condition nor the amount of time individuals spent in close proximity to the alpha within their main indoor/outdoor enclosure (Table 3). Correlation coefficients did not differ significantly between the Face-Direct and Full Body-Direct conditions ($z = 0.46$, $P = 0.65$), and between the Face-Averted and Full Body-Averted conditions ($z = 0.34$, $P = 0.73$). For all analyses, significance did not change when the four monkeys with prior photo experience were excluded (Table 1 in the Supplementary electronic materials).

At the LRC, the amount of time subjects spent in close proximity to the alpha within their main enclosure was not significantly related to subjects' latencies in the Face-Averted condition ($r = 0.10$, bootstrapped 95% CI: [−0.69, 0.99]) or in the Full Body-Averted condition ($r = -0.47$, bootstrapped 95% CI: [−0.93, 0.03]). The correlation coefficients from the Face-Averted and Full Body-Averted conditions did not significantly differ ($z = 0.85$, $P = 0.40$).

4. Discussion and conclusions

Questions about the ecological validity of using photos to study animal cognition and behaviour have already been reviewed in previous work (e.g. Fagot and Parron, 2010; Fagot et al., 2010; Bovet and Vauclair, 2000; Waitt and Buchanan-Smith, 2006). Our study, however, provides a rare test of the ecological validity of these methods by comparing subjects' behavioural reactions to social content depicted in photos with their behaviour towards the same social stimuli in real life. Contrary to our predictions, capuchins' responses to photos did not reflect their behaviour towards the real stimuli.

As previously discussed, wild and captive studies of brown capuchins show that relatively lower-ranking individuals often avoid close proximity to higher-ranking group members, presumably to avoid aggression (e.g. Fragaszy et al., 2004; Janson, 1990; Morton, 2014). This is particularly true in competitive situations, such as instances where two or more individuals are presented with a potentially monopolizable food source (as in the present study). The purpose of our testing whether latency to approach food was reflective of proximity to the alpha in the monkeys' main enclosures served only to demonstrate the behavioral validity of the measure, and thereby confirm what previous studies have already reported for alpha-subordinate capuchin relationships. Subjects' latencies to approach food inside the research cubicles when in the presence of the real alpha were negatively correlated with the amount of time subjects spent in close proximity to those individuals within their social group, i.e. a natural non-experimental setting. These results are consistent with previous work on wild and captive capuchins. Thus, while subjects at LL may have perceived the Plexiglas doors of the cubicles as a protective barrier to the photo stimuli and real monkey conditions (which were all placed in adjacent cubicles), latency to approach food inside the cubicles was an ecologically valid behaviour to compare with data on spatial proximity within their main enclosure.

Excluding monkeys with prior photo experience had no effect on the significance of the results and, as previously discussed, the experimental design of this study was completely novel to all subjects (Section 2.1). There were also no age-related differences in juveniles' and adults' responses to photos. Therefore, prior photo experience and developmental differences in photo perception cannot explain our results (e.g. Rosenfeld and Van Hoesen, 1979; Schell et al., 2011).

At LL, subjects' responses in the Face-Direct were shorter compared to their responses to the Full Body-Direct condition. Also, at the LRC, subjects responses to the Face-Averted condition were shorter compared to their responses to the Full Body-Averted condition. Such findings may be due to the fact that the floating face conditions were considerably smaller. Capuchins may have approached the full body conditions more slowly possibly because they were acting more cautious and/or were more curious or distracted by the larger stimuli. Regardless of why, however, capuchins may have needed more time to process the visual information in front of them, hence why they showed longer latencies to approach the food reward in those conditions.

At LL, subjects' responses in the Face-Direct and Full Body-Direct conditions differed significantly from their responses to the Face-Averted and Full Body-Averted conditions. One possibility is that, like most Old World primates, direct eye gaze is perceived as a threatening gesture among capuchins, and therefore the capuchins of our study showed longer latencies to approach photo conditions with direct eye gaze compared to photos with averted eye gaze. Alternatively, the monkeys may have quickly become habituated to photos with repeated exposure (see Fagot and Parron, 2010; Rosenfeld and Van Hoesen, 1979), which could have affected the LL monkeys' latencies during the Face-Averted and Full Body-Averted conditions (which were presented to them after the Face-Direct and Full Body-Direct conditions). Nevertheless, regardless of the underlying reason for these results, the LRC subjects were only presented with the Face-Averted and Full Body-Averted conditions, yet they did not respond to photos as they did towards the same individuals in real life. Therefore, any possible effects of habituation are unlikely to have affected our ability to test the main hypotheses of this study.

The angle between the observer and each test subject meant that we could not always determine the exact time when subjects first made visual contact with the photos, which may have affected our latency calculations. However, it seems unlikely, albeit not entirely possible to rule out, that the monkeys did not detect the photos upon entering the cubicles. For one, experimenters waited until subjects were looking in the direction of cubicle B before opening the door. Second, monkeys were trained prior to testing so they knew where to look for food in the cubicle (which we placed near each photo). Lastly, based on eye gaze and head angle, it was clear that in all trials, subjects were viewing the general direction of the photos as they approached the food. A large, conspicuous and novel object placed in close proximity to the food would very likely have captured their attention.

Several reasons might explain why the capuchins in this study did not respond to the stimuli in photos in the same way as they did to real life animals. The most obvious reason is that in the absence of other sensory cues like noise, movement, and smell, subjects were fully aware that the photos were not real and thus did not respond to them as such. Second, our subjects may have been deterred by the photo stimuli. There is a phenomenon in both humans and other primates called the "uncanny valley," in which subjects respond with notable aversion to stimuli that are too lifelike (Mori, 1970; Steckenfinger and Ghazanfar, 2009). It is possible that in our effort to create extremely lifelike images, we inadvertently created images that were perplexing or off-putting. The fact that subjects' latencies were substantial in the case of full body images may indicate that this effect, or something like it, influenced our results. Third, of course, it is possible that there is something fundamentally different about how capuchins process photos compared to real conspecifics, which could explain why our subjects had very different behavioural reactions to images compared to the real animals. This is perhaps the most troubling conclusion and, for reasons already discussed (Section 1), should be an important reminder that care is needed when interpreting animals' responses to photos. For example, Fagot et al. (2010) propose three levels of pictorial processing in animals: (1) confusion (i.e. the animal responds to the photo as if it were real), (2) independence (i.e. the animal makes no connection between the image and its content), and (3) equivalence (i.e. the photo is "read" as a representation of its referent, but is not perceived as the real thing). As noted previously, capuchins appear capable of recognizing conspecifics in photos (Pokorny and de Waal, 2009), and therefore are unlikely to perceive photos independent of their content. Also, since our study subjects did not respond to photos as if they were real individuals, it suggests that photos do not elicit a confusion response in these animals. Although further research is needed, these findings collectively suggest that capuchins may process photos under an "equivalence" mode as defined by Fagot et al. (2010) (see also Truppa et al., 2009), and therefore did not treat them as "real animals".

The purpose of replicating the Face-Averted and Full Body-Averted conditions with the LRC monkeys was to test our hypotheses involving these conditions within a sample of monkeys who were completely naïve to the study and its methods. In other words, due to possible order effects at Living Links, by replicating these conditions (which were administered to the LL monkeys after the Face-Direct and Full Body-Direct conditions) we could test our hypotheses in the relative absence of any bias due to order effects. While indeed site differences in variables like subjects' age, housing condition, relationship quality toward their group's alpha, and prior experience with photos may underlie the observed differences found between the LL and LRC monkeys' responses to the Face-Averted and Full Body-Averted conditions, our main point remains: If monkeys (in general) respond to photos in a way that reflects how they respond to the same stimuli in real life, then monkeys from both sites should have done so. This was not the case in the present study, and only furthers our argument that it is essential that researchers remain cautious when interpreting the behavioural and cognitive underpinnings of their animal subjects' responses to photos.

4.1. Future directions

Photos may enable researchers to identify particular aspects of animal social cognition and behaviour that would otherwise be difficult to test in real life, particularly natural settings. For example, in the case of primate eye gaze, lower-ranking individuals may not have the opportunity or the willingness to closely study the face of an alpha due to the associated risks (i.e. conflict from direct eye gaze; Hauser, 1996; van Hoof, 1967). However, based on our example, we believe that it is very important to use caution when interpreting the social relevance of such results since it is unclear what aspects of photo stimuli those animals are using when deciding how to behave. As previously discussed, it is rare for researchers to compare subjects' responses to photos with the same stimuli in real life. Further work is therefore needed to determine how animals interpret the social content of photo stimuli.

It would be interesting to test whether monkeys are more likely to respond to photos as they would live stimuli when exposed to a less or non-competitive situation. Capuchins likely rely on using social cues to gauge whether or not they should approach an alpha group member, and as we already have discussed, the lack of certain cues in photos (e.g. movement, smell) may result in different behavioural responses compared to when the real individual is present. This may not be the case in a non-competitive situation, where the subjects may not be as concerned or as focused on the movements and eye gaze of the alpha. Testing a similar set of conditions in a less competitive context could potentially result in different findings related to similarities and differences between photos and real stimuli.

An important limitation to our study is that with only a small number of participants in this study, statistical power may have been too low to detect significant differences between subjects' responses to photos and their responses to the same stimuli in real life. We attempted to reduce this risk by bootstrapping our analyses (Brownstone and Valletta, 2001). However, due to the low sample size, and the fact that this study was conducted on a single nonhuman primate species, our study should only serve as a stepping-stone for future studies to discuss and improve upon. We strongly encourage further work using a larger sample of participants, ideally covering a range of species that differ in their sensory perception (e.g. birds, dogs, rodents, primates).

Printed photo stimuli were used in this study in an attempt to provide a direct comparison to our real monkey condition within the cubicles. We encourage further work on a broader range of experimental conditions, particularly computerized presentation, which are commonly used by researchers but rarely placed in "realistic" locations (e.g. on a table placed outside the testing cubicle).

Although our study focused specifically on photos, we encourage similar work on other types of visual media, particularly videos. Unlike photos, videos are of course more realistic in terms of their depiction of motion and sound, which in turn may increase their ecological validity to test subjects. For instance, Shimizu (1998) found that male rock doves (*Columba livia*) respond to videos of female conspecifics using similar displays compared to their behaviour towards the same females in real life. Collectively, we look forward to future work that will highlight the best ways of using visual media technology to study animal social behaviour and cognition.

Conflict of interest

All authors declare no conflicts of interest.

Acknowledgements

We thank Prof. Andrew Whiten, Director of Living Links, for permission to conduct research at this facility, and to all of the staff for their support and assistance, particularly Lara Wood, Alison Dowling, and Sophie Pearson. We are especially grateful to RZSS Edinburgh Zoo for permission to work within the zoo. We thank Catherine Talbot for providing photos from the LRC, Lauren Robinson and Kelly Leverett for coding video for inter-observer reliability testing, and Kelly Leverett for completing the behavioural observations at the LRC. We are grateful to Valentina Truppa, Laura Wood, Sophia Daoudi, and the anonymous reviewers for providing useful comments on earlier drafts.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.beproc.2015.10.005.

References

Alfaro, J.W.L., E Silva Jr., J.S., Rylands, A.B., 2012. How different are robust and gracile capuchin monkeys? An argument for the use of *Sapajus* and *Cebus*. Am. J. Primatol., http://dx.doi.org/10.1002/ajp.22007.

ASAB, 2012. Guidelines for the treatment of animals in behavioural research and teaching. Anim. Behav. 83, 301–309.

Bovet, D., Vauclair, J., 2000. Picture recognition in animals and humans. Behav. Brain Res. 109, 143–165.

Brownstone, D., Valletta, R., 2001. The bootstrap and multiple imputations: harnessing increased computing power for improved statistical tests. J. Econ. Perspect. 15, 129–141.

D'Amato, M.R., Van Sant, P., 1988. The person concept in monkeys (*Cebus apella*). J. Exp. Psychol.: Anim. Behav. Processes 14, 43–55.

Davison, A.C., Hinkley, D.V., 1997. Bootstrap Methods and Their Applications. Cambridge University Press, Cambridge, ISBN 0-521-57391-2.

Efron, B., 1987. Better bootstrap confidence intervals. J. Am. Stat. Assoc. 82 (397), 171–185, http://dx.doi.org/10.2307/2289144.

Fagot, J., Parron, C., 2010. Picture perception in birds: perspective from primatologists. Comp. Cogn. Behav. Rev. 5, 132–135.

Fagot, J., Thompson, R.K.R., Parron, C., 2010. How to read a picture: lessons from nonhuman primates. PNAS 107 (2), 519–520.

Fragaszy, D.M., Visalberghi, E., Fedigan, L.M., 2004. The Complete Capuchin: The Biology of the Genus *Cebus*. Cambridge University Press, New York, NY.

Griffey, 2011. Human and non-human primate preferences for faces and facial attractiveness. In: PhD Thesis. University of Stirling, UK.

Guo, K., Robertson, R.G., Mahmoodi, S., Tadmor Young, M.P., 2003. How do monkeys view faces?—a study of eye movements. Exp. Brain Res. 150, 363–374.

Hauser, M.D., 1996. The Evolution of Communication. MIT Press, Cambridge, MA.

Janson, C.H., 1990. Social correlates of individual spatial choice in foraging groups of brown capuchin monkeys, *Cebus apella*. Anim. Behav. 40, 910–921.

Kyes, R.C., Candland, D.K., 1987. Baboon (*Papio hamadryas*) visual preference for regions of the face. J. Comp. Psychol. 101, 345–348.

Lefevre, C.E., Wilson, V.A.D., Morton, F.B., Brosnan, S.F., Paukner, A., Bates, T.C., 2014. Facial width-to-height ratio relates to alpha status and assertive personality in capuchin monkeys. PLoS One, http://dx.doi.org/10.1371/journal.pone.0093369.

Leonardi, R., Buchanan-Smith, H.M., Dufour, V., MacDonald, C., Whiten, A., 2010. Living together: behavior and welfare in single and mixed species groups of capuchin (*Cebus apella*) and squirrel monkeys (*Saimiri sciureus*). Am. J. Primatol. 72, 33–47.

MacDonald, C., Whiten, A., 2011. The 'Living Links to Human Evolution' research centre in Edinburgh zoo: a new endeavour in collaboration. Int. Zoo Yearb. 45, 7–17.

Martin, P., Bateson, P., 2007. Measuring Behaviour: An Introductory Guide. Cambridge University Press, Cambridge, UK, http://dx.doi.org/10.1017/CBO9780511810893.

Mori, M., 1970. The uncanny valley. Energy 7, 33–35.

Morton, F.B., 2014. Individual differences in learning, personality, and social success in brown capuchin monkeys (Sapajus sp.). Doctoral thesis submitted to the University of Stirling, UK. http://dspace.stir.ac.uk/handle/1893/21886?mode=full#.Vlh-FoQiolI.

Morton, F.B., Lee, P.C., Buchanan-Smith, H.M., Brosnan, S.F., Thierry, B., Paukner, A., de Waal, F.B., Widness, J., Essler, J.L., Weiss, A., 2013. Personality structure in brown capuchin monkeys (*Sapajus apella*): comparisons with chimpanzees (*Pan troglodytes*), orangutans (*Pongo* spp.), and rhesus macaques (*Macaca mulatta*). J. Comp. Psychol. 127, 282–298.

Müller, C.A., Schmitt, K., Barber, A.L.A., Huber, L., 2015. Dogs can discriminate emotional expressions of human faces. Curr. Biol. 25, 601–605.

Perret, A., Henry, L., Coulon, M., Caudal, J.-P., Richard, J.-P., Cousillas, H., Hausberger, M., George, I., 2015. Social visual contact, a primary drive for social animals? Anim. Cogn., http://dx.doi.org/10.1007/s10071-015-0834-8.

Pflüger, L.S., Valuch, C., Gutleb, D.R., Ansorge, U., Wallner, B., 2014. Colour and contrast of female faces: attraction of attention and its dependence on male hormone status in *Macaca fuscata*. Anim. Behav. 94, 61–71.

Pokorny, J.J., de Waal, F.B.M., 2009. Monkeys recognize the faces of group mates in photographs. PNAS 106 (51), 21539–21543.

Rosenfeld, S.A., Van Hoesen, G.W., 1979. Face recognition in the rhesus monkey. Neuropsychologia 17, 503–509.

Rowland, D.A., Perrett, D.I., 1995. Manipulating facial appearances through shape and color. IEEE Comput. Graph. Appl. 15 (5), 70–76.

Schell, A., Rieck, K., Schell, K., Hammerschmidt, K., Fischer, J., 2011. Adult but not juvenile *Barbary macaques* spontaneously recognize group member from pictures. Anim. Cogn. 14, 503–509.

Shimizu, T., 1998. Conspecific recognition in pigeons (*Columbia libia*) using dynamic video images. Behaviour 135, 43–53.

Steckenfinger, S.A., Ghazanfar, A.A., 2009. Monkey visual behavior falls into the uncanny valley. PNAS 106 (43), 18362–18366.

Truppa, V., Spinozzi, G., Stegagno, T., Fagot, J., 2009. Picture processing in tufted capuchin monkeys (*Cebus apella*). Behav. Processes 82, 140–152.

van Hoof, J.A.R.A.M., 1967. The facial displays for the catarrhine monkeys and apes. In: Morris, D. (Ed.), Primate Ethology. Aldine Publishing Company, Chicago, pp. 7–68.

Vandenheede, M., Bouissou, M.F., 1994. Fear reactions of ewes to photographic images. Behav. Processes 32, 17–28.

Vandenheede, M., Bouissou, M.F., 1995. Fear reactions of domestic sheep confronted with either a human or a human-like model. Behav. Processes 34, 81–92.

Waitt, C., Buchanan-Smith, H.M., 2006. Perceptual considerations in the use of colored photographic and video stimuli to study nonhuman primate behavior. Am. J. Primatol. 68, 1054–1067.

Waitt, C., Little, A.C., 2006. Preferences for symmetry in conspecific facial shape among *Macaca mulatta*. Int. J. Primatol. 27 (1), 133–145.

Waitt, C., Little, A.C., Wolfensohn, S., Honess, P., Brown, A.P., Buchanan-Smith, H., Perrett, D.I., 2003. Evidence from rhesus macaques suggests that male coloration plays a role in female mate choice. Biol. Lett., http://dx.doi.org/10.1098/rsbl.2003.0065.

Chimpanzee Personality and the Arginine Vasopressin Receptor 1A Genotype

V. Wilson[1,2,3], A. Weiss[1,3,*], T. Humle[4], N. Morimura[5], T.
Udono[5], G. Idani[5], T. Matsuzawa[6,7,8], S. Hirata[5], M. Inoue-Murayama[5,9]

[1]Department of Psychology, School of Philosophy, Psychology and Language Sciences, The University of Edinburgh

[2]Cognitive Ethology Laboratory, German Primate Center, Georg-August-Universität Göttingen and Leibniz-ScienceCampus Primate Cognition

[3]Scottish Primate Research Group

[4]DICE, School of Anthropology and Conservation, University of Kent

[5]Wildlife Research Center, Kyoto University

[6]Primate Research Institute, Kyoto University

[7]Japan Monkey Centre

[8]Institute for Advanced Study, Kyoto University

[9]National Institute for Environmental Studies

[*]Corresponding author: Email: alex.weiss@ed.ac.uk. Phone: + 44 131 650 3456. FAX: +44 131 650 3461. Postal address: 7 George Square, The University of Edinburgh, Edinburgh, EH8 9JZ, United Kingdom

Abstract

Polymorphisms of the arginine vasopressin receptor 1a (AVPR1a) gene have been linked to various measures related to human social behavior, including sibling conflict and agreeableness. In chimpanzees, AVPR1a polymorphisms have been associated with traits important for social interactions, including sociability, joint attention, dominance, conscientiousness, and hierarchical personality dimensions named low alpha/stability, disinhibition, and negative emotionality/low dominance. We examined associations between AVPR1a and six personality domains and hierarchical personality dimensions in 129 chimpanzees (*Pan troglodytes*) living in Japan or in a sanctuary in Guinea. We fit three linear and three animal models. The first model included genotype, the second included sex and genotype, and the third included genotype, sex, and sex × genotype. All personality phenotypes were heritable. Chimpanzees possessing the long form of the allele were higher in conscientiousness, but only in models that did not include the other predictors; however, additional analyses suggested that this may have been a consequence of study design. In animal models that included sex and sex × genotype, chimpanzees homozygous for the short form of the allele were higher in extraversion. Taken with the findings of previous studies of chimpanzees and humans, the findings related to conscientiousness suggest that AVPR1a may be related to lower levels of impulsive aggression. The direction of the association between AVPR1a genotype and extraversion ran counter to what one would expect if AVPR1a was related to social behaviors. These results help us further understand the genetic basis of personality in chimpanzees.

Key words: animal model, AVPR1a, chimpanzee, heritability, personality, vasopressin

Introduction

Arginine vasopressin is a neuropeptide involved in the regulation of the hypothalamic-pituitary-adrenal axis implicated in species differences in affiliative and aggressive behaviors (Bielsky et al. 2004). Vasopressin has three receptor types. Two of these receptors (AVPR1a and AVPR1b) have been implicated in social behavior, although the majority of this work has been focused on AVPR1a (Bielsky et al. 2004, Caldwell et al. 2008, Wersinger et al. 2002). In prairie voles (*Microtus ochrogaster*), a species with strong partner preferences, a repeat sequence of a microsatellite region in the 5’ flanking region of AVPR1a gene is present; this repeat sequence is shorter in montane voles (*M. montanus*), a closely-related species which does not form strong partner preferences (Nair and Young 2006). However, further analyses of AVPR1a across 21 *Microtus* species did not find an association between partner preferences and the AVPR1a genotype (Fink et al. 2006).

Recent research into cooperative breeding of cichlids also found species-specific differences in vasotocin expression relative to prosocial behavior; when social species were compared with non-social species, brain expression of vasotocin was higher for some social versus non-social species, but this pattern was not consistent across species (O'Connor et al. 2015). Similarly, a study of AVPR1a polymorphisms across three species of Old World monkeys (family Cercopithecidae), three species of gibbon (family Hylobatidae), and five great ape species (family Hominidae) found no association between the receptor polymorphism and mating behavior (Rosso et al. 2008). The authors did note however that they did not examine brain distributions of AVPR1a receptors in relation to species-specific behavior, an important consideration for understanding links between genotype, neurobiology and behavior (Rosso et al. 2008). The evidence that vasopressin and its homologs mediate species differences in vertebrate social behavior is therefore mixed.

Researchers have also examined within-species associations between vasopressin and behavior. Early work assessed the association between vasopressin and scent marking in Syrian hamsters

(*Mesocricetus auratus*). Scent marking in Syrian hamsters is higher in high ranking individuals, and vasopressin injections made into the medial preoptic area of the hypothalamus led to increases in scent marking (Ferris et al. 1984). Later studies of Syrian hamsters found that orally administered AVPR1a antagonists inhibit male aggression (Ferris et al. 2006). Similar results have recently been found in cooperatively breeding cichlids (*Neolamprologus pulcher*), with brain expression of vasotocin being higher in subordinate individuals (Reddon et al. 2015).

Studies also focused on the role of vasopressin in modulating behavioral pathways in humans. For example, intranasal administrations of vasopressin produced an increase in salivary cortisol during social stress (Ebstein et al. 2009), and were associated with reciprocity of cooperation in men (Rilling et al. 2012), and enhanced encoding of emotionally valenced facial expressions (Guastella et al. 2010). The role of vasopressin in emotion processing has further been linked to changes in prefrontal cortex and amygdala activation during a facial expression matching task (Zink et al. 2010).

Findings in humans, as well as those showing links between AVPR1a polymorphisms, vasopressin, and social behavior in nonhuman animals (e.g., Nair and Young 2006) encouraged researchers to carry out candidate gene studies of AVPR1a polymorphisms in humans. In humans, the RS3 microsatellite occurs within the Dup B region of the vasopressin receptor gene (Thibonnier et al. 2000), and is accompanied by the Dup A region (Donaldson et al. 2008), as in other great apes (Donaldson et al. 2008, Hammock and Young 2005). Several studies reported links between AVPR1a genotype and human behavior and personality. For example, men who are carriers of the RS3 334 bp allele of AVPR1a scored lower on a scale that assessed affiliation towards and time spent with their partner (Walum et al. 2008). The RS3 region has also been linked to traits of social appropriateness and sibling conflict (Bachner-Melman et al. 2005), and long forms of the RS3 region (i.e. 327-343 bp) have been associated with higher levels of AVPR1a mRNA in the hippocampus (Knafo et al. 2008). Of the few studies that examined links between AVPR1a and personality, one found an association between a non-synonymous SNP located on the vasopressin gene and higher agreeableness; however, this effect did not survive correction for multiple tests (Haram et al. 2014). Additionally, a gene enrichment analysis of candidate genes for aggression found an association between AVPR1a and aggression in nearly 19,000 children (Pappa et al. 2016).

Recent studies examined the role of AVPR1a polymorphisms in the behavior and personality of chimpanzees. Unlike humans and other great apes, chimpanzees are polymorphic for the deletion of the Dup B site, including the RS3 microsatellite (Donaldson et al. 2008, Hammock and Young 2005). Hopkins et al. (2012) and Latzman et al. (2014) examined associations between polymorphisms of the Dup B region of AVPR1a and personality in 83 and 116 chimpanzees, respectively. The personality domains used in Hopkins et al. (2012) were based on a four component structure that was found in chimpanzees at the Yerkes National Primate Center and chimpanzees housed in U.S. and Australian zoological parks (see Weiss et al. 2007 for details). The personality variables used in Latzman et al. (2014) represented hierarchical personality dimensions derived using a two-step procedure (see Goldberg 2006 for details). In the first step principal components analyses were used to extract and obtain component scores for two, three, four, five, and six component solutions. In the second step correlations between component scores that represented associations between components at higher and lower levels of the hierarchy, i.e., between component scores from structures with fewer and more dimensions, respectively, were computed. In these studies, Hopkins et al. (2012) and Latzman et al. (2014) did not find significant main effects of genotype, but they did find significant sex × by genotype interactions. Specifically, Hopkins et al. (2012) found that, among chimpanzees who possessed the long form of the Dup B allele, males scored higher than females on the dominance domain and lower than females on the conscientiousness domain. Similarly, Latzman et al. (2014) found that the male advantage in the hierarchical personality dimensions “(low) Alpha/Stability” and “Disinhibition” at the levels of the two- and three-component levels, respectively, was greater among chimpanzees who possessed the long form of the Dup B allele.

Latzman et al. also found that the female advantage in a hierarchical personality dimension at the three-component level, “negative emotionality/low Dominance,” was greater among chimpanzees who possessed the long form of the Dup B allele.

Three further studies of this AVPR1a polymorphism in chimpanzees demonstrate its association with traits related to social behavior. Hopkins et al. (2014) found significant sex, genotype, and the sex × genotype interaction effects on performance in a receptive joint attention task: males with the long form of the Dup B allele demonstrated better performance than males who were homozygous for the deletion. Anestis et al. (2014) found that chimpanzees with a copy of the *L* allele (lacking the RS3 deletion) had higher scores on “smart” (“uses coalitions”, “receives grooming often”, “frequently initiates play”) and in males, higher scores on “friendly” (“directs affiliative behavior to others”) (see their Table II). Finally, Staes et al. (2015) reported that male chimpanzees homozygous for the long allele, and female heterozygotes, groomed and were groomed by others more frequently.

Building on these findings, and especially the work of Hopkins et al. (2012) and Latzman et al. (2014), we tested whether the long form of the AVPR1a genotype was associated with any of the six chimpanzee personality domains---dominance, extraversion, conscientiousness, agreeableness, neuroticism, and openness---identified in an earlier study (King and Figueredo 1997) or the hierarchical personality dimensions of (low) Alpha/Stability, Disinhibition, and negative emotionality/low Dominance, that were related to genotype in Latzman et al. (2014). Because these and other studies found evidence for sex × genotype interactions, we also tested for this interaction.

Our study differed in two ways from the work of Hopkins et al. (2012) and Latzman et al. (2014). Firstly, we used a more recent version of the personality questionnaire than did the studies of Hopkins et al. (2012) and Latzman et al. (2014). Our questionnaire thus included 11 additional items (see Weiss et al. 2009 for details). Furthermore, unlike Hopkins et al. (2012) we tested for associations between genotype and all six personality domains, and not just the dominance, extraversion, conscientiousness, and agreeableness domains, which generalized from chimpanzees living in zoos in the United States and Australia to chimpanzees living in Yerkes National Primate Center (Weiss et al. 2007).

The second difference concerns our analytic approach. Hopkins et al. (2012) and Latzman et al. (2014) tested for associations between personality constructs and genotypes by means of linear models (multivariate analyses of covariance) followed by univariate analyses of covariance. In both cases, to adjust for relatedness, the models included a covariate that indicated, for each chimpanzee, his or her relatedness with all other chimpanzees in their pedigree. Furthermore, Latzman et al. (2014) but not Hopkins et al. (2012) tested for rearing history effects and the two- and three-way interactions between sex, rearing history, and genotype. For our study we also fit linear models, but we did not include rearing effects because Latzman et al. (2014) did not find any significant main effects of rearing or interactions of rearing with sex or genotype. In addition, unlike Latzman et al. (2014) and Hopkins et al. (2012), but similar to (Hopkins et al. 2014), we controlled for relatedness by fitting ‘animal models’. The animal model is a type of mixed effects model in which the degree to which subjects deviate from the mean on some trait, i.e., the random effects of individuals, are not treated as independent, but as being more similar between genetically related individuals (Kruuk 2004). The animal model accomplishes this by using a matrix that describes the genetic relatedness (Wright’s coefficient of relatedness) between all pairs of individuals to estimate how much each individual deviates from the trait’s mean (Kruuk 2004). As such, when fixed effects, such as genotype, are included in an animal model, the relatedness among all pairs of individuals is taken into account. In other words, these models can estimate the effects of a candidate gene on a phenotype while controlling for the tendency for related individuals to resemble one another more closely on that phenotype *and* to be more likely to share the candidate gene (Kruuk 2004). Animal models therefore eliminate the possibility that the phenotype and gene are inherited together but are not causally related and thus provides a robust method for assessing personality-genotype relationships in samples of related individuals (Kruuk 2004). One further benefit of animal models is that, because they provide an estimate of the additive genetic variance underlying the phenotype under study, they provide heritability estimates. Given the small number of studies on the heritability of personality in chimpanzees (Latzman et al. 2015, Weiss et al. 2000), obtaining heritability estimates of chimpanzee personality in another sample will be valuable.

Methods

Subjects

Subjects were drawn from chimpanzees in zoological parks, research centers, and a sanctuary, all located in Japan (N = 124), or in a sanctuary in Guinea (N = 19). To avoid stratification, we excluded chimpanzees whose subspecies was not *Pan troglodytes verus* (1 *P. t. schweinfurthii*, 1 *P. t. troglodytes*, 10 hybrids, and 2 unknown). The remaining 129 chimpanzees (69 females and 60 males) included 110 chimpanzees who lived in 11 facilities in Japan and the 19 wild chimpanzees in Guinea. The ages of the chimpanzees ranged from 1.7 to 51.7 (mean ± SD = 20.5 ± 10.7).

Genotypes

DNA was extracted from blood or fecal samples (Hong et al. 2009). Genotyping of the AVPR1a DupB region was conducted following Latzman et al. (2014). We used a forward primer 5’-GCATGGTAGCCTCTCTTTAAT-3’ and a reverse primer 5’-CATACACATGGAAAGCACCTAA-3’ (synthesized following Donaldson et al. 2008) and *LA-Taq* DNA polymerase (TaKaRa, Shiga, Japan) for PCR amplification with an annealing temperature of 55° C for 35-40 cycles. PCR products were resolved on a 2% agarose gel. The DupB-containing allele (*L*) resulted in a band of 900 base pairs, while the DupB minus allele (*S*) was 570 base pairs long. Genotyping was repeated at least twice to check the result.

A total of 145 chimpanzees were initially genotyped. The genotypes of two chimpanzees were uncertain. We excluded these individuals. Of the 129 successfully genotyped chimpanzees who were *P. t. verus*, 94 were homozygous for the S allele (*SS*), 5 were homozygous for the L allele (*LL*), and 30 were heterozygous (*LS*). Because of the low number of *LL* chimpanzees, we conducted an exact test

(Graffelman and Morales-Camarena 2008) using the HardyWeinberg package (Graffelman 2015) in R (R Core Team 2015) to test whether these genotypes were in Hardy-Weinberg equilibrium. The SELOME p-value (0.19) indicated that these genotypes were in Hardy-Weinberg equilibrium. The less conservative mid p-value (0.13) arrived at the same conclusion.

Personality ratings

Chimpanzees were rated on the Hominoid Personality Questionnaire (HPQ; Weiss et al. 2009), an expanded version of the Chimpanzee Personality Questionnaire and the Orangutan Personality Questionnaire (for details see King and Figueredo 1997, Weiss et al. 2006). The Chimpanzee Personality Questionnaire was used in the previous studies on AVPR1a genotype and personality (Hopkins et al. 2012, Latzman et al. 2014).

The HPQ consists of 54 trait descriptive adjectives followed by one to three sentences that set the adjective in the context of primate behavior. For example, the item 'fearful' reads "**FEARFUL**: Subject reacts excessively to real or imagined threats by displaying behaviors such as screaming, grimacing, running away or other signs of anxiety or distress." The questionnaire instructs raters to use a 7-point scale to rate chimpanzees on the item where "1" is defined as "Displays either total absence or negligible amounts of the trait" and "7" is defined as "Displays extremely large amounts of the trait." Raters were also instructed not to discuss their ratings.

The chimpanzees in Japan and in Guinea were rated on a Japanese and French translation of the HPQ, respectively. The psychometric properties of the Japanese translation were comparable to the English language version of the Chimpanzee Personality Questionnaire (Weiss et al. 2009). The psychometric properties of a French translation of the Chimpanzee Personality Questionnaire, which was not used in this study, were comparable to the English language version of the same questionnaire (King et al. 2005).

Analyses

Variables. The dependent variables were standardized scores representing the six chimpanzee personality domains described by Weiss et al. (2009) and three hierarchical personality dimensions---low alpha, disinhibition, and negative emotionality/low dominance---described by Latzman et al. (2014). To create the dependent personality variables, we first obtained mean item scores across raters. We then used these scores to create unit-weighted scores for each domain or dimension (see ESM Table 1). For ease of interpretation, we transformed these variables into *z*-scores (mean ± SD = 0 ± 1). The independent variables included sex (female = 0, male = 1) and genotype (*L* carriers = 0, *SS* = 1).

Modeling. Statistical analyses were conducted using R (R Core Team 2015). To test whether personality domains were associated with the AVPR1a genotype we first fit three linear models for each personality variable using the lm function (R Core Team 2015). The first linear model included genotype as the sole effect, the second linear model included the effects of sex and genotype, and the third linear model included the effects of sex, genotype, and sex × genotype.

We then fit three animal models for each personality variable using the MCMCglmm function (Hadfield 2010). These models were identical to the linear models in that the first included the fixed effect of genotype as the sole effect, the second included the fixed effects of sex and genotype, and the third included the fixed effects of sex, genotype, and the sex × genotype interaction. All three animal models also included subject identity as a random effects term that was conditioned on the relatedness matrix, which was generated by MCMCglmm from our chimpanzee pedigree. The paternity and maternity data in this pedigree for the 129 chimpanzees housed in Japan were obtained from the Great Ape Information Network (http://www.shigen.nig.ac.jp/gain/index.jsp). The sire and dam were known for 68 subjects, providing pedigree data for 90 chimpanzees. Sire and dam were unknown for all 19 chimpanzees in Guinea. To estimate fixed and random effects, MCMCglmm uses Markov Chain Monte Carlo estimation to determine the parameters of a posterior distribution and uses an inverse-Gamma distribution as the prior for variance components (Hadfield 2010). We specified priors with a belief parameter (v) of 0.75 and a covariance matrix (**V**) of 0.5. We ran the models for 10,000,000 iterations, had a burn in period of 6,000,000, and thinned the samples from the posterior distribution to 1000.

Results

*Linear Model*s

The results for the linear models are presented in Table 1. There were significant sex effects. In models that only adjusted for sex, males were higher in dominance, lower in conscientiousness, higher in low alpha and disinhibition, and lower in negative emotionality/low dominance. In the fully adjusted models, males were higher in extraversion, lower in conscientiousness, higher in low alpha, and higher in disinhibition. There was only one significant effect of genotype: in the unadjusted model, subjects who were homozygous for the *S* allele were lower in conscientiousness than those who were *L* allele carriers. None of the sex × genotype interaction effects were significant.

*Animal Model*s

The trace plots for the animal models did not suggest the presence of autocorrelations and the density plots indicated that the distributions around the estimates were approximately normal. Data used to create trace and density plots are available at https://github.com/alexweissuk/avpr1a-chimpanzee.git.

The personality domains and the hierarchical personality dimensions were heritable in all models. The heritabilities across models and phenotypes ranged from 0.13 to 0.44, the median heritability was 0.24, and none of the critical intervals included 0 (see Table 2).

The results of the animal models are presented in Table 3. As in the linear models, there were significant sex effects. In sex adjusted models males were higher in dominance, lower in conscientiousness, and higher in low alpha and disinhibition. In fully adjusted models, males were higher in extraversion, lower in conscientiousness, and again, higher in low alpha and disinhibition. There were also two significant effects of genotype. First, in the unadjusted model subjects who were homozygous for the *S* allele were lower in conscientiousness than those who were *L* allele carriers (see Figure 1). Second, in the fully adjusted model subjects who were homozygous for the *S* allele were higher in extraversion than those who were *L* allele carriers. As in our linear models, none of the sex × genotype interactions were significant.

Supplementary Analyses

Because the results of our linear models and our animal models differed from those of Hopkins et al. (2012) and Latzman et al. (2014), we used our data to test whether differences between our study and the earlier studies are responsible for these contrasting findings. The first difference was that our sample included 19 chimpanzees from Guinea who were orphaned early in life. The effect of being orphaned may have influenced the development of these chimpanzees either alone or via gene × environment interactions (Suomi 2006). So far as we are aware, the samples studied by Hopkins et al. (2012) and Latzman et al. (2014) did not include chimpanzees who were orphaned early in life, and they were all captive-housed. Another difference was that the chimpanzees in the present study were assessed using a 54 item questionnaire that defined six components. The chimpanzees in the Hopkins et al. (2012) study were assessed using the 43 item Chimpanzee Personality Questionnaire and the four domains examined in their study (Weiss et al. 2007) differed some from their counterparts in our study.

To test whether these differences explain why we did not find the same results as did Hopkins et al. (2012) and Latzman et al. (2014), we fit animal models that included sex, genotype, and sex × genotype as fixed effects, and subject ID conditioned by relatedness as a random effect. Our priors, covariance matrix, number of iterations, burn in period, and thinning were identical to our main analyses. However, for these animal models, we excluded the 19 chimpanzees from Guinea and used unit-weighted scores for dominance and conscientiousness domains that were identical to those described by Hopkins et al. (2012) (see ESM Table 1). Trace plots did not suggest the presence of autocorrelations and density plots indicated that the distributions around the estimates were approximately normal. Again, data used to create these plots are available at https://github.com/alexweissuk/avpr1a-chimpanzee.git. The analyses indicated that males were significantly higher than females in low alpha; none of the other fixed effects of sex nor the effects of genotype and the sex × genotype interaction were significant (see Table 4).

One further possibility is that differences in the distribution of chimpanzees and raters across facilities led to our results. Specifically, in contrast to Hopkins et al. (2012) and Latzman et al. (2014), where all of the chimpanzees belonged to a single facility and their personalities were assessed by a largely overlapping set of raters, although the majority of our captive sample ($n = 77$) were housed in a single sanctuary and had their personalities assessed by one group of raters, 33 chimpanzees were housed across 10 institutions, each with a different set of raters. To test whether this explained our results we fit a linear model and animal model that included the effects of sex, genotype, and sex × genotype in the chimpanzees who lived in the sanctuary. For these analyses we focused on the version of the conscientiousness domain examined by Hopkins et al. (2012). The linear model revealed that males were rated as significantly lower in conscientiousness than females ($b = -0.91$, 95% CI = -1.80 to -0.02, $p = 0.044$), that chimpanzees homozygous for the short form of the allele were significantly lower in conscientiousness than chimpanzees who possessed the long form ($b = -0.73$, 95% CI = -1.37 to -0.08, $p = 0.028$), and that there was no significant sex × genotype interaction ($b = 0.76$, 95% CI = -0.27 to 1.79). Trace plots for the animal model did not suggest the presence of autocorrelations and density plots indicated that the distributions around the estimates were approximately normal. Again, the data used to create these plots is available at https://github.com/alexweissuk/avpr1a-chimpanzee.git. The animal model results were similar: chimpanzees who had lower conscientiousness scores were male ($b = -1.06$, 95% CI = -1.96 to -0.13, $n_{eff} = 3898$, $p_{MCMC} = 0.026$) and possessed the *SS* genotype ($b = -0.71$, 95% CI = -1.43 to -0.08, $n_{eff} = 4000$, $p_{MCMC} = 0.043$). Once again, interaction was not significant ($b = 0.93$, 95% CI = -0.10 to 1.98, $n_{eff} = 4000$, $p_{MCMC} = 0.0860$).

Discussion

We found an association between higher conscientiousness and the long form of the AVPR1a gene in a linear model and in an animal model. In both cases, the effect of genotype was not significant when adjusting for sex or for sex and sex × genotype, although supplementary analyses suggested that this may be attributable to the way that the chimpanzees and raters in our study were distributed across facilities. We also found that *S* homozygotes were higher in extraversion. We found no evidence for associations between AVPR1a genotype and the dominance, agreeableness, neuroticism, and openness domains or the hierarchical personality dimensions. The narrow sense heritabilities of all six personality domains and the three hierarchical personality dimensions were significant.

Previous studies of chimpanzees found that the long form of AVPR1a was associated with dominance and conscientiousness (Hopkins et al. 2012), and hierarchical personality dimensions related that captured conscientiousness- and dominance-related traits (Latzman et al. 2014), but that the direction of these effects differed between males and females. Other findings in chimpanzees found associations between the long form of the gene and better performance in a joint attention task (Hopkins et al. 2014), a tendency to use coalitions and receive positive attention from conspecifics and, among males, to have many friends (Anestis et al. 2014), and a higher frequency of allogrooming (Staes et al. 2015). Studies of humans found an association between the AVPR1a genotype and aggression in children similar to what has been found in other species (Pappa et al. 2016), and an association between the long allele of the RS3 region and altruistic behavior, and increased expression of AVPR1a mRNA in the hippocampus (Knafo et al. 2008).

A study of captive chimpanzees found an association between conscientiousness and lower levels of agonistic behavior (Pederson et al. 2005) and a content analysis of conscientiousness revealed one facet related to predictability and low impulsivity and another related to low levels of aggression (King and Weiss 2011). These findings, then, along with the above-described studies of chimpanzees and humans, suggest that the long form of the AVPR1a gene acts to reduce levels of impulsive aggression. The long form of the AVPR1a gene, then, might reduce impulsive aggression by promoting social perception (Hopkins et al. 2014) and/or promoting socially appropriate behavior (Anestis et al. 2014, Bachner-Melman et al. 2005, Staes et al. 2015).

On the other hand, some of our findings do not mesh well with what we would expect based on previous findings. For one, our finding that *L* carriers were lower in extraversion is the opposite of what would be expected from a gene that is related to social behaviors and also findings that chimpanzees who possess the long form of AVPR1a exhibit higher levels of allogrooming (Staes et al. 2015). One possibility is that the traits captured by chimpanzee (Freeman and Gosling 2010, King and Figueredo 1997, Weiss et al. 2009, Weiss et al. 2007) and human extraversion (Costa and McCrae 1995), for example, gregariousness, activity, and positive affect, have a different and opposite association with the long form of AVPR1a than do traits related to socially appropriate behaviors, such as a tendency to avoid unnecessary aggression. However, because this association was only significant in an animal model that adjusted for sex and sex × genotype and its effect size was larger in these models than in the unadjusted and the sex-adjusted models, we would advise caution in interpreting this result until it can be examined in further studies or in a meta-analysis.

Another puzzling finding was that unlike Hopkins et al. (2012) and Latzman et al. (2014) we did not find evidence for sex × genotype effects for conscientiousness, dominance, or the hierarchical personality dimensions. Results from our first supplementary analyses suggested that these null results were not attributable to the dominance and conscientiousness scales used or our inclusion of a group of wild, orphaned chimpanzees. In addition, our second supplementary analyses could not clearly rule out (or in) the possibility that the way in which chimpanzees and raters were distributed across facilities in our study led to our null findings with respect to whether the effects of genotype on conscientiousness differs between males and females. Of course, one remaining possibility to explain our discrepant findings is that we used animal models to control for relatedness whereas Hopkins et al. (2012) and (Latzman et al. 2014) did not. However, we do not think this is likely given that Hopkins et al. (2014) found a significant sex by AVPR1a genotype interaction using an analysis method that controlled for relatedness in much the same way as does the animal model (Almasy and Blangero 1998). Given these findings, we do not think that methodological differences between our study and those of Hopkins et al. (2012) and Latzman et al. (2014) can explain our somewhat different results. Further research on larger samples, preferably assessed by the same group of raters, is thus needed to resolve this question.

In addition to the findings related to the AVPR1a genotype and personality domains and hierarchical personality dimensions, the evidence for the heritability of all of the personality phenotypes is consistent with studies of humans (Bouchard and Loehlin 2001), orangutans (Adams et al. 2012), rhesus macaques (Brent et al. 2014), and chimpanzees (Latzman et al. 2015, Weiss et al. 2000). Weiss et al. (2000) reported a heritability of 0.63 for chimpanzee dominance, an estimate higher than that reported here. The same study also found no evidence for the heritability of the other factors. One possible reason for this difference may be that the prior study used symmetric differences squared, which relies on ordinary least squares regression (Grimes and Harvey 1980). In contrast, the present study implemented the animal model using Bayesian analysis, which performs better when sample sizes are low (O'Hara et al. 2008).

Trying to understand the genetic basis of complex traits has given rise to debate over the best approach to assessing personality-genotype associations; some argue that genome-wide association studies are preferable to candidate gene studies because they account for the fact that complex traits may be influenced by small effects of multiple genes (Chabris et al. 2012). However, a genome wide association study of chimpanzees or any other great ape species is not feasible as obtaining sufficient sample sizes for such studies would be impossible. Furthermore, candidate gene studies are beneficial if they are hypothesis-driven and selection of the candidate gene is based on knowledge of the functional role of the polymorphism (Tabor et al. 2002). Thus candidate gene studies, including attempts to replicate findings, may complement genome-wide association studies (Reif and Lesch 2003).

Understanding differences in the association between AVPR1a and social behavior across species has important consequences for how we understand the evolution of group cohesion and cooperation. High powered studies testing for associations between AVPR1a and personality measures that are standardized across species would be beneficial to this end.

Acknowledgments

We thank staff at the different sites for completing questionnaires and for providing genetic samples. This study was financially supported by the Cooperation Research Program of the Primate Research Center, Kyoto University, and the Japan Society for the Promotion of Science (JSPS) Grant-in-Aids for Scientific Research Nos. 25118005 and 25290082 to MI-M, and JSPS Short-term Postdoctoral Fellowship for North American and European Researchers (No. PE14030) to VW. Data collection was also funded by funding by The University of Edinburgh Development Trust (No. 2828) and the Daiwa Anglo-Japanese Foundation (No. 6515/6818) to AW. A visit to Japan by AW was generously supported by the Leading Graduate Program in Primatology and Wildlife Science. We thank Mr. Yuuki Makimura and Ms. Hiromi Kobayashi for their technical support. We are also grateful to Mark James Adams for his assistance in conducting and interpreting the results of the MCMCglmm analyses.

Table 1: Linear model results for the effects of AVPR1 genotype, sex, and sex × genotype on personality domains and hierarchical personality dimensions

	Unadjusted				Sex adjusted				Fully adjusted			
	b	SE	l-95%	u-95%	b	SE	l-95%	u-95%	b	SE	l-95%	u-95%
Dominance												
Intercept	-0.12	0.17	-0.46	0.21	-0.30	0.18	-0.65	0.05	-0.36	0.21	-0.77	0.05
SS vs. *LL*+*LS*	0.17	0.20	-0.23	0.56	0.10	0.19	-0.28	0.49	0.19	0.25	-0.31	0.69
Sex	---	---	---	---	**0.49**	**0.17**	**0.14**	**0.83**	0.64	0.34	-0.04	1.32
SS vs. *LL*+*LS* × Sex	---	---	---	---	---	---	---	---	-0.21	0.40	-0.99	0.58
Extraversion												
Intercept	-0.14	0.17	-0.48	0.19	-0.22	0.18	-0.58	0.14	-0.44	0.21	-0.85	-0.02
SS vs. *LL*+*LS*	0.20	0.20	-0.19	0.59	0.17	0.20	-0.22	0.57	0.49	0.26	-0.01	1.00
Sex	---	---	---	---	0.20	0.18	-0.15	0.55	**0.78**	**0.35**	**0.10**	**1.47**
SS vs. *LL*+*LS* × Sex	---	---	---	---	---	---	---	---	-0.79	0.40	-1.59	0.00
Conscientiousness												
Intercept	0.33	0.17	-0.00	0.65	0.59	0.17	0.25	0.92	0.63	0.20	0.24	1.02
SS vs. *LL*+*LS*	**-0.45**	**0.19**	**-0.83**	**-0.06**	-0.36	0.18	-0.72	0.01	-0.42	0.24	-0.89	0.06
Sex	---	---	---	---	**-0.70**	**0.16**	**-1.02**	**-0.38**	**-0.81**	**0.32**	**-1.45**	**-0.17**
SS vs. *LL*+*LS* × Sex	---	---	---	---	---	---	---	---	0.15	0.38	-0.59	0.90
Agreeableness												
Intercept	-0.16	0.17	-0.49	0.18	-0.16	0.18	-0.52	0.20	-0.18	0.21	-0.60	0.25
SS vs. *LL*+*LS*	0.22	0.20	-0.18	0.61	0.21	0.20	-0.18	0.61	0.23	0.26	-0.28	0.75
Sex	---	---	---	---	0.02	0.18	-0.34	0.37	0.05	0.35	-0.65	0.75
SS vs. *LL*+*LS* × Sex	---	---	---	---	---	---	---	---	-0.04	0.41	-0.85	0.77

Neuroticism												
Intercept	-0.13	0.17	-0.46	0.21	-0.13	0.18	-0.49	0.23	-0.24	0.21	-0.67	0.18
SS vs. *LL*+*LS*	0.17	0.20	-0.22	0.56	0.17	0.20	-0.23	0.57	0.34	0.26	-0.18	0.85
Sex	---	---	---	---	0.01	0.18	-0.34	0.37	0.32	0.35	-0.38	1.02
SS vs. *LL*+*LS* × Sex	---	---	---	---	---	---	---	---	-0.41	0.41	-1.22	0.39
Openness												
Intercept	0.01	0.17	-0.33	0.35	0.05	0.18	-0.31	0.41	0.04	0.22	-0.39	0.46
SS vs. *LL*+*LS*	-0.01	0.20	-0.41	0.38	0.00	0.20	-0.40	0.40	0.02	0.26	-0.50	0.53
Sex	---	---	---	---	-0.10	0.18	-0.46	0.25	-0.07	0.35	-0.77	0.63
SS vs. *LL*+*LS* × Sex	---	---	---	---	---	---	---	---	-0.04	0.41	-0.86	0.77
Low Alpha												
Intercept	-0.19	0.17	-0.52	0.14	-0.41	0.17	-0.76	-0.07	-0.48	0.20	-0.88	-0.08
SS vs. *LL*+*LS*	0.26	0.20	-0.13	0.65	0.18	0.19	-0.19	0.56	0.28	0.25	-0.21	0.77
Sex	---	---	---	---	**0.60**	**0.17**	**0.27**	**0.94**	**0.78**	**0.33**	**0.12**	**1.44**
SS vs. *LL*+*LS* × Sex	---	---	---	---	---	---	---	---	-0.24	0.39	-1.01	0.53
Disinhibition												
Intercept	-0.21	0.17	-0.54	0.12	-0.39	0.18	-0.74	-0.05	-0.48	0.21	-0.89	-0.07
SS vs. *LL*+*LS*	0.29	0.20	-0.10	0.68	0.23	0.19	-0.16	0.61	0.35	0.25	-0.15	0.84
Sex	---	---	---	---	**0.49**	**0.17**	**0.15**	**0.83**	**0.71**	**0.34**	**0.04**	**1.39**
SS vs. *LL*+*LS* × Sex	---	---	---	---	---	---	---	---	-0.30	0.39	-1.08	0.48

Negative Emotionality/Low Dominance												
Intercept	0.06	0.17	-0.28	0.39	0.24	0.18	-0.11	0.59	0.24	0.21	-0.17	0.66
SS vs. *LL+LS*	-0.08	0.20	-0.47	0.32	-0.01	0.19	-0.40	0.37	-0.02	0.25	-0.52	0.48
Sex	---	---	---	---	**-0.49**	**0.17**	**-0.83**	**-0.15**	-0.51	0.34	-1.19	0.17
SS vs. *LL+LS* × Sex	---	---	---	---	---	---	---	---	0.02	0.40	-0.77	0.81

Note. Personality domains and hierarchical personality dimensions were converted into z-scores for these analyses. l-95% and u-95% represent the lower and upper bounds of the 95% confidence interval, respectively. Significant values highlighted in bold ($p < 0.05$).

Table 2: Heritability estimates for each personality domain and hierarchical personality dimensions

	Unadjusted			Sex adjusted			Fu*LL*y adjusted		
Domains	h^2	l-95%	u-95%	h^2	l-95%	u-95%	h^2	l-95%	u-95%
Dominance	0.24	0.04	0.44	0.21	0.04	0.41	0.21	0.04	0.41
Extraversion	0.44	0.10	0.76	0.42	0.10	0.75	0.41	0.10	0.74
Conscientiousness	0.19	0.03	0.41	0.21	0.04	0.44	0.21	0.03	0.44
Agreeableness	0.28	0.04	0.56	0.28	0.04	0.57	0.28	0.04	0.57
Neuroticism	0.14	0.03	0.28	0.14	0.03	0.28	0.13	0.03	0.27
Openness	0.25	0.04	0.52	0.27	0.04	0.57	0.27	0.04	0.57
Hierarchical dimensions									
Low Alpha	0.27	0.04	0.55	0.27	0.06	0.56	0.27	0.05	0.55
Disinhibition	0.23	0.03	0.49	0.24	0.04	0.50	0.25	0.04	0.51
Negative Emotionality/Low Dominance	0.17	0.04	0.35	0.16	0.03	0.31	0.16	0.03	0.32

Note. l-95% and u-95% represent the lower and upper bounds of the 95% confidence interval, respectively.

Table 3: MCMCglmm results for the effects of AVPR1 genotype, sex, and sex × genotype on personality domains and hierarchical personality dimensions

	Unadjusted				Sex adjusted				Fu*LL*y adjusted			
	b	l-95%	u-95%	N_{eff}	b	l-95%	u-95%	N_{eff}	b	l-95%	u-95%	N_{eff}
Dominance												
Intercept	-0.10	-0.45	0.24	4000.00	-0.26	-0.62	0.11	4622.37	-0.32	-0.72	0.10	4000.00
SS vs. *LL*+*LS*	0.13	-0.26	0.54	4000.00	0.07	-0.33	0.46	4671.12	0.16	-0.28	0.69	3513.66
Sex	---	---	---	---	**0.44**	**0.09**	**0.78**	**4000.00**	0.60	-0.06	1.26	4000.00
SS vs. *LL*+*LS* × Sex	---	---	---	---	---	---	---	---	-0.22	-0.93	0.59	3818.62
Extraversion												
Intercept	-0.19	-0.56	0.15	4000.00	-0.23	-0.60	0.14	4000.00	-0.44	-0.89	-0.02	4000.00
SS vs. *LL*+*LS*	0.25	-0.15	0.64	4000.00	0.22	-0.20	0.60	4000.00	**0.54**	**0.01**	**1.06**	**4000.00**
Sex	---	---	---	---	0.14	-0.20	0.49	4000.00	**0.68**	**0.02**	**1.34**	**4000.00**
SS vs. *LL*+*LS* × Sex	---	---	---	---	---	---	---	---	-0.73	-1.48	0.05	4000.00
Conscientiousness												
Intercept	0.36	-0.00	0.69	3621.01	0.61	0.27	0.96	4189.74	0.65	0.27	1.08	4000.00
SS vs. *LL*+*LS*	**-0.44**	**-0.82**	**-0.03**	**4166.38**	-0.35	-0.73	0.01	4233.38	-0.41	-0.88	0.09	3739.51
Sex	---	---	---	---	**-0.71**	**-1.05**	**-0.39**	**3210.01**	**-0.83**	**-1.50**	**-0.19**	**3818.34**
SS vs. *LL*+*LS* × Sex	---	---	---	---	---	---	---	---	0.16	-0.60	0.90	3791.20
Agreeableness												
Intercept	-0.15	-0.51	0.21	4000.00	-0.15	-0.50	0.23	4000.00	-0.16	-0.59	0.27	4000.00
SS vs. *LL*+*LS*	0.25	-0.15	0.66	4000.00	0.25	-0.14	0.66	4000.00	0.27	-0.24	0.78	4000.00
Sex	---	---	---	---	0.01	-0.35	0.35	4000.00	0.05	-0.64	0.75	3919.04
SS vs. *LL*+*LS* × Sex	---	---	---	---	---	---	---	---	-0.06	-0.90	0.71	4000.00

Neuroticism												
Intercept	-0.13	-0.48	0.21	3795.22	-0.15	-0.53	0.21	4000.00	-0.25	-0.66	0.18	4000.00
SS vs. *LL*+*LS*	0.15	-0.27	0.55	4000.00	0.15	-0.23	0.58	4000.00	0.31	-0.20	0.82	4000.00
Sex	---	---	---	---	0.03	-0.30	0.40	4000.00	0.32	-0.37	1.01	3210.06
SS vs. *LL*+*LS* × Sex	---	---	---	---	---	---	---	---	-0.39	-1.20	0.40	3070.15
Openness												
Intercept	-0.02	-0.38	0.31	4000.00	0.03	-0.33	0.41	4000.00	0.03	-0.41	0.45	4000.00
SS vs. *LL*+*LS*	0.03	-0.37	0.44	4000.00	0.05	-0.34	0.47	4000.00	0.05	-0.46	0.59	4000.00
Sex	---	---	---	---	-0.15	-0.51	0.20	4000.00	-0.15	-0.86	0.53	4000.00
SS vs. *LL*+*LS* × Sex	---	---	---	---	---	---	---	---	0.01	-0.83	0.79	4000.00
low Alpha												
Intercept	-0.18	-0.54	0.16	4000.00	-0.40	-0.76	-0.04	4000.00	-0.47	-0.88	-0.03	4000.00
SS vs. *LL*+*LS*	0.20	-0.19	0.62	4000.00	0.13	-0.26	0.52	4146.43	0.24	-0.26	0.74	4354.32
Sex	---	---	---	---	**0.59**	**0.26**	**0.95**	**4000.00**	**0.78**	**0.11**	**1.41**	**3711.00**
SS vs. *LL*+*LS* × Sex	---	---	---	---	---	---	---	---	-0.25	-1.01	0.50	4000.00
Disinhibition												
Intercept	-0.22	-0.57	0.13	4000.00	-0.41	-0.78	-0.05	4177.15	-0.49	-0.87	-0.05	4000.00
SS vs. *LL*+*LS*	0.26	-0.16	0.65	3693.09	0.20	-0.20	0.59	4369.26	0.32	-0.18	0.80	4000.00
Sex	---	---	---	---	**0.50**	**0.16**	**0.85**	**3742.39**	**0.73**	**0.09**	**1.37**	**4000.00**
SS vs. *LL*+*LS* × Sex	---	---	---	---	---	---	---	---	-0.32	-1.04	0.45	4000.00

Negative Emotionality/ Low Dominance												
Intercept	0.03	-0.32	0.37	4000.00	0.21	-0.17	0.58	4000.00	0.22	-0.18	0.66	4000.00
SS vs. *LL*+*LS*	-0.05	-0.47	0.35	4000.00	0.00	-0.41	0.38	4000.00	-0.01	-0.50	0.50	4231.06
Sex	---	---	---	---	-0.46	-0.82	-0.12	4000.00	-0.50	-1.14	0.22	4000.00
SS vs. *LL*+*LS* × Sex	---	---	---	---	---	---	---	---	0.05	-0.71	0.87	4000.00

Note. Personality domains and hierarchical personality dimensions were converted into z-scores for these analyses. l-95% and u-95% represent the lower and upper bounds of the 95% credible interval, respectively. N_{eff} = effective sample size. Significant values highlighted in bold ($p < 0.05$).

Table 4: MCMCglmm results for the effects of AVPR1 genotype, sex, and sex × genotype on personality domains and hierarchical personality dimensions when personality domains were defined as they were in Weiss et al. (2007) and chimpanzees living in Guinea are excluded

	b	l-95%	u-95%	N_{eff}
Dominance				
Intercept	-0.30	-0.75	0.16	4000.00
SS vs. *LL*+*LS*	0.05	-0.48	0.60	4000.00
Sex	0.70	-0.05	1.45	3812.24
SS vs. *LL*+*LS* × Sex	-0.15	-0.96	0.77	4000.00
Conscientiousness				
Intercept	0.55	0.10	1.00	4000.00
SS vs. *LL*+*LS*	-0.46	-1.01	0.10	4000.00
Sex	-0.62	-1.38	0.15	4000.00
SS vs. *LL*+*LS* × Sex	0.22	-0.65	1.04	4000.00
low Alpha				
Intercept	-0.47	-0.93	-0.03	4000.00
SS vs. *LL*+*LS*	0.31	-0.27	0.83	3822.28
Sex	**0.77**	**0.08**	**1.56**	**4287.68**
SS vs. *LL*+*LS* × Sex	-0.30	-1.12	0.54	4090.68
Disinhibition				
Intercept	-0.47	-0.90	-0.00	4000.00
SS vs. *LL*+*LS*	0.41	-0.11	0.99	4000.00
Sex	0.65	-0.07	1.43	3578.12
SS vs. *LL*+*LS* × Sex	-0.33	-1.18	0.54	3419.31
Negative Emotionality / Low Dominance				
Intercept	0.21	-0.24	0.65	3945.26
SS vs. *LL*+*LS*	0.03	-0.49	0.58	4105.81
Sex	-0.62	-1.35	0.13	4000.00
SS vs. *LL*+*LS* × Sex	0.12	-0.72	0.98	3875.40

Note. Personality domains and hierarchical personality dimensions were converted into z-scores for these analyses. l-95% and u-95% represent the lower and upper bounds of the 95% credible interval, respectively. N_{eff} = effective sample size. Significant values highlighted in bold ($p < 0.05$).

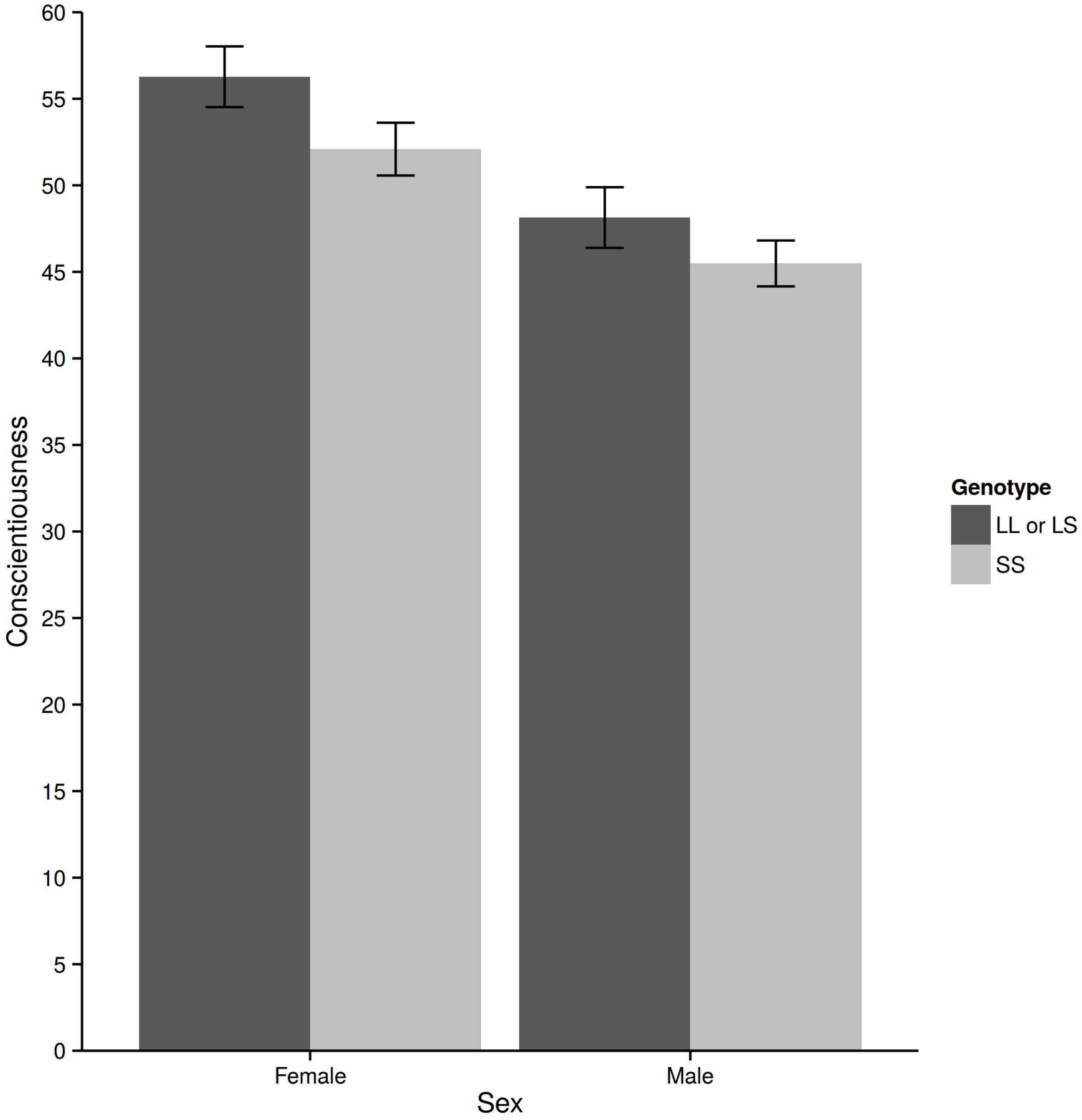


Figure 1: Mean conscientiousness scores in *T*-score units (mean ± SD = 50 ± 10) for males and females by AVPR1a genotype. Error bars represent standard errors.

Electronic Supplementary Material Table 1: Unit weighted items for each chimpanzee personality domain, for the six factor structure (Weiss et al. 2009), four factor structure (Hopkins et al. 2012) and the three hierarchical personality dimensions (Latzman et al. 2014)

	Six factor structure		**Four item structure**	
	Loading		Loading	
Domain^{a}	Positive	Negative	Positive	Negative
Dominance	Dominant	Submissive	Dominant	Submissive
	Independent	Dependent	Independent	Dependent
	Decisive	Fearful	Decisive	Fearful
	Intelligent	Timid	Persistent	Timid
	Persistent	Cautious	Bullying	Cautious
	Bullying	Vulnerable		
	Stingy	Anxious		
	Manipulative			
Extraversion	Active	Solitary	Active	Solitary
	Playful	Lazy	Playful	Lazy
	Social	Individualistic	Sociable	Depressed
	Friendly	Depressed	Friendly	Unemotional
	Affectionate		Affectionate	
	Imitative		Inquisitive	
			Inventive	
			Imitative	
Conscientiousness	Predictable	Impulsive	Predictable	Impulsive

		Defiant	Stable	Defiant
		Reckless	Gentle	Reckless
		Erratic		Erratic
		Irritable		Irritable
		Aggressive		Aggressive
		Jealous		Jealous
		Disorganized		Disorganized
		Thoughtless		Clumsy
		Distractible		Depressed
		Unperceptive		Excitable
		Quitting		Autistic
		Clumsy		Stingy
				Manipulative
Agreeableness	Sympathetic		Sympathetic	
	Helpful		Helpful	
	Sensitive		Sensitive	
	Protective		Protective	
	Gentle		Gentle	
	Conventional		Sociable	
			Friendly	
			Affectionate	
			Stable	
			Predictable	
			Intelligent	

Neuroticism	Excitable	Stable
	Autistic	Cool
Openness	Inquisitive	
	Inventive	
	Curious	
	Innovative	
Hierarchical dimension[b]	Positive	Negative
Disinhibition	Impulsive	Stable
	Erratic	Gentle
	Reckless	Sympathetic
	Excitable	Friendly
	Irritable	Predictable
	Aggressive	Affectionate
	Bullying	
	Defiant	
	Jealous	
	Stingy	
Negative Emotionality	Dependent	Bullying
	Submissive	Independent
	Timid	Dominant
	Fearful	Decisive
	Cautious	

Low Alpha	Aggressive	Gentle
	Bullying	Cautious
	Reckless	Submissive
	Defiant	Sympathetic
	Dominant	Dependent
	Stingy	Stable
	Irritable	Friendly
	Impulsive	
	Jealous	
	Persistent	
	Erratic	
	Excitable	
	Independent	

Note. [a]Item weights generated from loadings ≥ |0.4|; [b]Item weights generated from loadings ≥ |0.5| as in Latzman et al. (2014).

References

Adams MJ, King JE, Weiss A (2012) The majority of genetic variation in orangutan personality and subjective well-being is nonadditive. Behav Genet 42:675-686

Almasy L, Blangero J (1998) Multipoint quantitative-trait linkage analysis in general pedigrees. American Journal of Human Genetics 62:1198-1211

Anestis SF, Webster TH, Kamilar JM, et al. (2014) AVPR1A variation in chimpanzees (*Pan troglodytes*): Population differences and association with behavioral style. International Journal of Primatology 35:305-324

Bachner-Melman R, Zohar AH, Bacon-Shnoor N, et al. (2005) Link between vasopressin receptor AVPR1A promoter region microsatellites and measures of social behavior in humans. Journal of Individual Differences 26:2-10

Bielsky IF, Hu SB, Szegda KL, et al. (2004) Profound impairment in social recognition and reduction in anxiety-like behavior in vasopressin V1a receptor knockout mice. Neuropsychopharmacology 29:483-493

Bouchard TJ, Jr., Loehlin JC (2001) Genes, evolution, personality. Behavior Genetics 31:243-273

Brent LJ, Semple S, Maclarnon A, et al. (2014) Personality traits in rhesus macaques (*Macaca mulatta*) are heritable but do not predict reproductive output. International Journal of Primatology 35:188-209

Caldwell HK, Wersinger SR, Young WS (2008) The role of the vasopressin 1b receptor in aggression and other social behaviours. In: Neumann ID, Landgraf R (eds) Advances in Vasopressin and Oxytocin — From Genes to Behaviour to Disease. Elsevier B. V., Amsterdam, pp. 65-72

Chabris CF, Hebert BM, Benjamin DJ, et al. (2012) Most reported genetic associations with general intelligence are probably false positives. Psychological Science 23:1314-1323

Costa PT, Jr., McCrae RR (1995) Domains and facets: Hierarchical personality assessment using the Revised NEO Personality Inventory. J Pers Assess 64:21-50

Donaldson ZR, Kondrashov FA, Putnam A, et al. (2008) Evolution of a behavior-linked microsatellite-containing element in the 5' flanking region of the primate AVPR1A gene. BMC Evolutionary Biology 8:180

Ebstein RP, Israel S, Lerer E, et al. (2009) Arginine vasopressin and oxytocin modulate human social behavior. Ann N Y Acad Sci 1167:87-102

Ferris CF, Albers HE, Wesolowski SM, et al. (1984) Vasopressin injected into the hypothalamus triggers a stereotypic behavior in golden hamsters. Science 224:521-523

Ferris CF, Lu SF, Messenger T, et al. (2006) Orally active vasopressin V1a receptor antagonist, SRX251, selectively blocks aggressive behavior. Pharmacology, Biochemistry, and Behavior 83:169-174

Fink S, Excoffier L, Heckel G (2006) Mammalian monogamy is not controlled by a single gene. Proceedings of the National Academy of Sciences of the United States of America 103:10956-10960

Freeman HD, Gosling SD (2010) Personality in nonhuman primates: A review and evaluation of past research. Am J Primatol 72:653-671

Goldberg LR (2006) Doing it all Bass-Ackwards: The development of hierarchical factor structures from the top down. J Res Pers 40:347-358

Graffelman J (2015) Exploring diallelic genetic markers: The HardyWeinberg Package. Journal of Statistical Software 64:1-22

Graffelman J, Morales-Camarena J (2008) Graphical tests for Hardy-Weinberg Equilibrium based on the ternary plot. Human Heredity, 65:77-84

Grimes LW, Harvey WR (1980) Estimation of genetic variances and covariances using symmetric differences squared. Journal of Animal Science 50:634-644

Guastella AJ, Kenyon AR, Alvares GA, et al. (2010) Intranasal arginine vasopressin enhances the encoding of happy and angry faces in humans. Biological Psychiatry 67:1220-1222

Hadfield J (2010) MCMC methods for Multi-response Generalized Linear Mixed Models: The MCMCglmm R Package. Journal of Statistical Software 33:1-22

Hammock EAD, Young LJ (2005) Microsatellite instability generates diversity in brain and sociobehavioral traits. Science 308:1630-1634

Haram M, Tesli M, Dieset I, et al. (2014) An attempt to identify single nucleotide polymorphisms contributing to possible relationships between personality traits and oxytocin-related genes. Neuropsychobiology 69:25-30

Hong KW, Matsukawa R, Hirata Y, et al. (2009) Allele distribution and effect on reporter gene expression of vasopressin receptor gene (AVPR1a)-linked VNTR in primates. Journal of Neural Transmission 116:535-538

Hopkins WD, Donaldson ZR, Young LJ (2012) A polymorphic indel containing the RS3 microsatellite in the 5' flanking region of the vasopressin V1a receptor gene is associated with chimpanzee (Pan troglodytes) personality. Genes Brain Behav 11:552-558

Hopkins WD, Keebaugh AC, Reamer LA, et al. (2014) Genetic influences on receptive joint attention in chimpanzees (*Pan troglodytes*). Scientific Reports 4

King JE, Figueredo AJ (1997) The Five-Factor Model plus Dominance in Chimpanzee Personality. Journal of Research in Personality 31:257-271

King JE, Weiss A (2011) Personality from the perspective of a primatologist. In: Weiss A, King JE, Murray L (eds) Personality and temperament in nonhuman primates. Springer, New York, pp. 77-99

King JE, Weiss A, Farmer KH (2005) A chimpanzee (*Pan troglodytes*) analogue of cross-national generalization of personality structure: Zoological parks and an African sanctuary. J Pers 73:389-410

Knafo A, Israel S, Darvasi A, et al. (2008) Individual differences in allocation of funds in the dictator game associated with length of the arginine vasopressin 1a receptor RS3 promoter region and correlation between RS3 length and hippocampal mRNA. Genes, Brain and Behavior 7:266-275

Kruuk LEB (2004) Estimating genetic parameters in natural populations using the ‘animal model’. Philosophical Transactions of the Royal Society B Biological Sciences 359:873-890

Latzman RD, Freeman HD, Schapiro SJ, et al. (2015) The contribution of genetics and early rearing experiences to hierarchical personality dimensions in chimpanzees (*Pan troglodytes*). J Pers Soc Psychol 109:889-900

Latzman RD, Hopkins WD, Keebaugh AC, et al. (2014) Personality in chimpanzees (Pan troglodytes): exploring the hierarchical structure and associations with the vasopressin V1A receptor gene. PLoS One 9:e95741

Nair HP, Young LJ (2006) Vasopressin and pair-bond formation: genes to brain to behavior. Physiology 21:146-152

O'Connor CM, Marsh-Rollo SE, Ghio SC, et al. (2015) Is there convergence in the molecular pathways underlying the repeated evolution of sociality in African cichlids? Hormones and Behavior 75:160-168

O'Hara RB, Cano JM, Ovaskainen O, et al. (2008) Bayesian approaches in evolutionary quantitative genetics. J Evol Biol 21:949-957

Pappa I, St Pourcain B, Benke K, et al. (2016) A genome-wide approach to children's aggressive behavior: The EAGLE consortium. American Journal of Medical Genetics Part B: Neuropsychiatric Genetics 171:562-572

Pederson AK, King JE, Landau VI (2005) Chimpanzee (*Pan troglodytes*) personality predicts behavior. Journal of Research in Personality 39:534-549

R Core Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Reddon AR, O'Connor CM, Marsh-Rollo SE, et al. (2015) Brain nonapeptide levels are related to social status and affiliative behaviour in a cooperatively breeding cichlid fish. Royal Society Open Science 2:140072

Reif A, Lesch K-P (2003) Toward a molecular architecture of personality. Behavioural Brain Research 139:1-20

Rilling JK, DeMarco AC, Hackett PD, et al. (2012) Effects of intranasal oxytocin and vasopressin on cooperative behavior and associated brain activity in men. Psychoneuroendocrinology 37:447-461

Rosso L, Keller L, Kaessmann H, et al. (2008) Mating system and avpr1a promoter variation in primates. Biology Letters 4:375-378

Staes N, Koski SE, Helsen P, et al. (2015) Chimpanzee sociability is associated with vasopressin (Avpr1a) but not oxytocin receptor gene (OXTR) variation. Hormones and Behavior 75:84-90

Suomi SJ (2006) Risk, resilience, and gene x environment interactions in rhesus monkeys. Ann N Y Acad Sci 1094:52-62

Tabor HK, Risch NJ, Myers RM (2002) Candidate-gene approaches for studying complex genetic traits: practical considerations. Nature Reviews Genetics 3:1-7

Thibonnier M, Graves MK, Wagner MS, et al. (2000) Study of V(1)-vascular vasopressin receptor gene microsatellite polymorphisms in human essential hypertension. Journal of Molecular and Cellular Cardiology 32:557-564

Walum H, Westberg L, Henningsson S, et al. (2008) Genetic variation in the vasopressin receptor 1a gene (AVPR1A) associates with pair-bonding behavior in humans. Proceedings of the National Academy of Sciences of the United States of America 105:14153-14156

Weiss A, Inoue-Murayama M, Hong KW, et al. (2009) Assessing chimpanzee personality and subjective well-being in Japan. Am J Primatol 71:283-292

Weiss A, King JE, Figueredo AJ (2000) The heritability of personality factors in chimpanzees (*Pan troglodytes*). Behavior Genetics 30:213-221

Weiss A, King JE, Hopkins WD (2007) A cross-setting study of chimpanzee (*Pan troglodytes*) personality structure and development: Zoological parks and Yerkes National Primate Research Center. Am J Primatol 69:1264-1277

Weiss A, King JE, Perkins L (2006) Personality and subjective well-being in orangutans (*Pongo pygmaeus* and *Pongo abelii*). Journal of Personality and Social Psychology 90:501-511

Wersinger SR, Ginns EI, O'Carroll A-M, et al. (2002) Vasopressin V1b receptor knockout reduces aggressive behavior in male mice. Mol Psychiatry 7:975-984

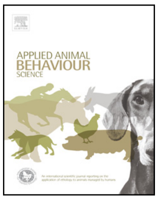
Zink CF, Stein JL, Kempf L, et al. (2010) Vasopressin modulates medial prefrontal cortex-amygdala circuitry during emotion processing in humans. The Journal of Neuroscience 30:7017-7022

Applied Animal Behaviour Science xxx (2016) xxx–xxx

Contents lists available at ScienceDirect

Applied Animal Behaviour Science

journal homepage: www.elsevier.com/locate/applanim



Happiness is positive welfare in brown capuchins (*Sapajus apella*)

Lauren M. Robinson[a,b,c,*], Natalie K. Waran[b], Matthew C. Leach[d], F. Blake Morton[c,e], Annika Paukner[f], Elizabeth Lonsdorf[e], Ian Handel[g], Vanessa A.D. Wilson[a,c], Sarah F. Brosnan[h], Alexander Weiss[a,c]

[a] *Department of Psychology, School of Philosophy, Psychology and Language Sciences, University of Edinburgh, 7 George Square, Edinburgh, EH8 9JZ, UK*
[b] *Jeanne Marchig International Centre for Animal Welfare Education, Royal (Dick) School of Veterinary Studies, The University of Edinburgh, Easter Bush Veterinary Centre, Roslin, EH25 9RG, UK*
[c] *Scottish Primate Research Group, Scotland, UK*
[d] *School of Agriculture, Food & Rural Development, Agriculture Building, Newcastle University, Newcastle upon Tyne, NE1 7RU, UK*
[e] *Department of Psychology, Franklin & Marshall College, Lancaster, PA, 17603, USA*
[f] *Laboratory of Comparative Ethology, Eunice Kennedy Shriver National Institute of Child Health and Human Development, Dickerson, MD 20842, USA*
[g] *The Roslin Institute and The Royal (Dick) School of Veterinary Studies, University of Edinburgh, Roslin, EH25 9RG, UK*
[h] *Department of Psychology, Georgia State University, Atlanta, GA 30303, USA*

ARTICLE INFO

Article history:
Received 17 December 2015
Received in revised form 21 May 2016
Accepted 29 May 2016
Available online xxx

Keywords:
Capuchin
Personality
Primate
Stereotypy
Subjective well-being
Welfare

ABSTRACT

Questionnaires that allow people who are familiar with individual animals to rate the welfare of these animals are an underutilised tool. We designed a 12-item welfare questionnaire and tested its reliability and associations with subjective well-being (SWB), locomotor stereotypy, and personality traits. The welfare questionnaire included questions relating to physical health, stress and coping, satisfaction with social relationships, psychological stimulation, and the display of positive and negative welfare indicators. We collected ratings of 66 brown capuchins (*Sapajus apella*) living in three facilities. Each capuchin was rated on the welfare questionnaire by an average of 2.8 raters. The interrater reliability of the welfare questionnaire items ranged from ICC(3,*k*) 0.51 to 0.86. A principal components analysis indicated that the 12 welfare items loaded onto one component. We repeated this process with the welfare and four items used to measure subjective well-being and found all the items were defined by a single component (welfareSWB). We then conducted three sets of analyses, one predicting the welfare component, one predicting the SWB component, and predicting the welfareSWB component. The independent variables were frequency of locomotor stereotypy, personality, age, and sex; facility was included as a random effect. In models including stereotypy, age, and sex we found frequency of stereotypy to be significantly associated with all three predicted components (ps < 0.01). After controlling for stereotypy ($b = -0.25$, $p = 0.17$), age ($b = -0.54$, $p = 0.01$), and sex ($b = -0.32$, $p = 0.07$), the personality traits of Sociability ($b = 1.02$, $p < 0.001$), Assertiveness, ($b = 0.63$, $p < 0.001$), and Attentiveness ($b = 0.54$, $p = 0.01$) were associated with higher scores on the joint welfareSWB component; Neuroticism was negatively associated with welfare SWB ($b = -0.60$, $p = 0.01$). Our results suggest that welfare questionnaires is a useful, reliable, and valid tool for primate welfare assessment.

1. Happiness is positive welfare in brown capuchins (*Sapajus apella*)

People working within animal facilities are an often underutilised source of knowledge for improving animal welfare. These people use their experience to collect and interpret new information and, when shared, their observations can be used to track animal welfare. However, in spite of these capabilities there are few studies using questionnaires to assess animal welfare.

The goal of our study was to test the utility of questionnaires as a tool for assessing nonhuman primate welfare. This is an increasingly important area of research given the growing interest in assuring the welfare of animals kept in research facilities. This is also important because in order to improve animal welfare we need to be able to accurately assess it. We chose to study brown capuchin monkeys (*Sapajus apella*) due to the large numbers in captivity (IUCN, 2014) and the fact that there has been extensive research on their behaviour and cognition (Fragaszy et al., 2004). In particular, the personality structure of brown capuchins has been studied

---

[*] Corresponding author at: School of Philosophy, Psychology and Language Sciences, University of Edinburgh, 7 George Square, Edinburgh, EH8 9JZ, UK.
E-mail address: l.robinson@ed.ac.uk (L.M. Robinson).

http://dx.doi.org/10.1016/j.applanim.2016.05.029
0168-1591/

(Morton et al., 2013), which presented the opportunity to study the association between ratings of welfare, subjective well-being, and personality.

Animal welfare is often assessed using physiological responses and behavioural observations (Broom and Johnson, 1993; Broom, 1988). These methods have drawbacks (Rushen, 1991). For example, blood draws may be stressful, which makes measures of glucocorticoids difficult to interpret (Laule et al., 2003). Behavioural observations, although they do not disrupt the animal, are time-consuming and need to be conducted multiple times to gain an accurate assessment of an individual's welfare state (Vazire et al., 2007). Alternatively, staff can fill out questionnaires, based on their daily observations of animals' behaviours and environmental responses, for a large number of animals in a time-efficient manner. As with other methods of welfare assessment, ratings are not perfect as raters may have individual biases. However, concerns about questionnaire reliability and validity can be assessed by testing the agreement between raters and whether responses are related to observed welfare states. If we can devise reliable and valid questionnaires for rating primate welfare, then facilities housing primates would have one more tool for monitoring and improving welfare.

One benefit of questionnaires is that they can cover several indicators and welfare states in a relatively short period of time. This is important because in order to effectively assess welfare it is crucial to assess multiple indices. For example, chronic stress is associated with reduced immune response (Broom, 2006; Cohen et al., 1992) and increased incidence of self-injury (Davenport et al., 2008; Lutz et al., 2003). There is also increased focus on accounting for the experience of positive emotions (or happiness) in welfare assessment (Boissy et al., 2007). A primate welfare questionnaire that covers a diverse set of welfare indicators, including those relating to both positive and negative welfare, could be used to further investigate how different aspects of welfare are interconnected.

One questionnaire designed to assess happiness in nonhuman primates is King and Landau's subjective well-being questionnnaire (SWB) (2003), which was based on studies of human happiness (Sandvik et al., 1993). This questionnaire was initially used to assess chimpanzees (King and Landau, 2003) and has since been used with other nonhuman primate species (Weiss et al., 2011a,b, 2006) and felids (Gartner and Weiss, 2013) and other nonhuman primates (Weiss et al., 2011a,b, 2006). These studies have shown that the interrater and retest reliabilities of animal SWB are similar to those of humans (Diener, 2009). Also, as in humans (Diener and Chan, 2011; Diener et al., 2003), happier animals (those with higher SWB) tend to live longer (Weiss et al., 2011a) and share certain personality traits, such as higher Extraversion (King and Landau, 2003; Weiss et al., 2009, 2006).

In humans happiness and welfare are directly associated with one another (Diener, 2009) suggesting that they are measuring similar constructs. Both animal welfare and SWB involve the animal's ability to cope with their environment and the balance of positive and negative experiences (Broom, 2007; King and Landau, 2003). Does this mean SWB is equivalent to animal welfare? By assessing welfare and SWB in brown capuchins, we can determine the degree to which these constructs are related in this species.

Accounting for variation in personality has been suggested as another way of understanding and improving captive animal welfare (Tetley and O'Hara, 2012). Studying personality and welfare together may help researchers better understand why animals in a shared environment may have different welfare states. Until now the five brown capuchin personality traits (Assertiveness, Openness, Neuroticism, Sociability, and Attentiveness) have not been studied in connection with welfare and SWB.

As such, in this study we assessed the reliability and validity of a 12-item welfare questionnaire in brown capuchins. We then examined the convergence of ratings of welfare and happiness. Finally, we tested the association of ratings of welfare and SWB with locomotor stereotypy and personality traits.

2. Methods

2.1. Ethical approval

This project was approved by the participating facilities in July 2014. This study was non-invasive and complied with the US Animal Welfare Act (USDA, 2008).

2.2. Subjects

Subjects were 66 brown capuchins (31 males) housed at the National Institutes of Health, Georgia State University, and Franklin & Marshall College. Ages ranged from 0.55 years to 45.56 years (mean ± SD = 12.47 years ± 9.03 years). Across the facilities all the capuchins were socially housed in groups or pairs.

2.3. Instruments

2.3.1. Welfare questionnaire

We designed the welfare questionnaire with practicality in mind, and so it was relatively brief and applicable to multiple primate species. The questionnaire is comprised of three sections. The first section asks raters, who were caretakers or other individuals with extensive experience working with the animals that they rated, to answer questions about their experience working with animals. In addition, to prime raters for the welfare questions, this section of the questionnaire asks which physical and behavioural indicators raters use to determine whether an animal has positive or negative welfare. The second section consisted of 12 questions based on the five major contributors to animal quality of life proposed by McMillan (2005), including social relationships, mental stimulation, health, stress, and control of the social and physical environment. Some of the definitions and wording were influenced by Broom (2007, 1991), Broom and Johnson (1993), and by Green and Mellor (2011). Each of the items could be rated on a five point Likert scale ranging from very bad to very good, altered to fit the question wording and to capture negative and positive welfare states (Boissy et al., 2007; Yeates and Main, 2008). Each question also included a section for comments. The welfare questionnaire is available in Supplementary materials.

2.3.2. Subjective well-being ratings

We collected subjective well-being ratings for the capuchins using King and Landau's four-item questionnaire[1] (2003). This questionnaire asks raters to estimate how often each animal is happy, how satisfying each animal finds their social experiences, how successful the animal is at achieving its goals, and to imagine how happy they would be if they were that animal for a week. Raters used a seven point Likert scale to rate how well each adjective describes the individual animals from "Displays either total absence or negligible amounts of the trait or state" to "Displays extremely large amounts of the trait".

2.3.3. Personality ratings

We collected personality ratings using the Hominoid Personality Questionnaire,[2] a 54-item questionnaire where each item consists of an adjective and one to three descriptive sentences (Weiss et al.,

---

[1] The SWB questionnaire can be found at http://extras.springer.com/2011/978-1-4614-0175-9/weiss_monkey_wellbeing.pdf.

[2] The HPQ can be found at http://extras.springer.com/2011/978-1-4614-0175-9/weiss_monkey_personality.pdf.

Please cite this article in press as: Robinson, L.M., et al., Happiness is positive welfare in brown capuchins (*Sapajus apella*). Appl. Anim. Behav. Sci. (2016), http://dx.doi.org/10.1016/j.applanim.2016.05.029

2011b). For example, the item *fearful* is "**FEARFUL:** 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 HPQ uses a seven point Likert scale from "Displays either total absence or negligible amounts of the trait" to "Displays extremely large amounts of the trait".

2.3.4. Stereotypic behaviour

We collected data on the frequency of locomotor stereotypy to test the welfare and SWB questionnaires' relation to an observable welfare state. We asked staff to "Rate how often each animal performs any of the following behaviours by placing an X in the appropriate column". This was followed by operational definitions taken from Vandeleest et al. (2011) for the following stereotypies: pace, flip, twirl, swing, bounce, head twist, and rock. Staff then rated each capuchins' stereotypic behaviour on a five point frequency scale from "never" to "constantly".

2.4. Data collection

We collected welfare questionnaires and subjective well-being ratings from 7 May 2014 to 28 August 2014. Ten raters performed 185 ratings of the 66 capuchins using the welfare questionnaire (mean = 2.80 ratings per capuchin); nine raters performed 181 ratings using the SWB questionnaire (mean = 2.70 ratings per capuchin). Raters knew each capuchin for an average of 3.88 years (range: 0.50–16 years, SD ± 3.81 years). There were 19 missing data points out of 2220 possible welfare responses and no missing data points out of 724 possible SWB responses. At the same time we collected 64 personality ratings of 18 animals. We used 140 personality ratings of 48 of these capuchins previously collected in 2010 and reported in Morton et al. (2013). Each of the 66 capuchins was rated on average 3.25 times; three animals were only rated once. Overall there were 230 missing data points out of 11016 possible personality responses. Lastly, in December, 2015 we collected 172 ratings of stereotypy frequency from seven raters (mean = 2.61 raters per animal); there were no missing data points. All seven raters had contributed to the 2014 data collection. Because we wanted to test the welfare and SWB questionnaires' validity by connecting them to an observable welfare state, we collected stereotypy ratings after we collected data from the questionnaires. Raters for all the questionnaires were researchers, care staff and/or students familiar with individual animals. For all the questionnaires any item with a missing value was replaced with that items' mean score (Downey and King, 1998).

2.5. Analysis

Statistical analyses were performed using R, version 3.1.1 (R Development Core Team, 2014).

2.5.1. Intraclass correlations

We used intraclass correlations (*ICC*s) to assess the interrater reliability of welfare and SWB ratings of the 48 animals that were assessed by multiple raters; the same animals were in both analyses. We also performed *ICC*s to assess the reliability of the personality items for the 63 capuchins that were assessed by multiple raters. *ICC*(3,1) estimates the reliability of single ratings and *ICC*(3,*k*) assesses the reliability across mean ratings based on *k* raters (Shrout and Fleiss, 1979).

2.5.2. Principal components analyses

We averaged the welfare item scores across raters leaving a single score per animal and then conducted separate principal component analyses (PCA) for the welfare items and the SWB items. We determined the number of components to extract by examining the scree plot and performing a parallel analysis (Dinno and Dinno, 2010; Horn, 1965). We then computed unit-weighted component scores (Gorsuch, 1983) by assigning a weight of +1 to loadings that were greater than or equal to 0.4 and a weight of −1 to loadings that were less than or equal to −0.4. All other loadings were assigned weights of 0. In the event that an item had a loading greater than or equal to |.4| on more than one component, we assigned the item to the component on which it had the highest loading. We then performed a joint-PCA with the 12 welfare items and the four SWB items.

Table 1
Interrater reliability of welfare and SWB items.

Item	ICC(3,1)	ICC(3,k)
Social control	0.63	0.86
Number of relationships	0.63	0.86
Physical health	0.56	0.82
Positive/negative experience	0.53	0.80
Quality of relationships	0.49	0.77
Positive welfare	0.46	0.75
Stress frequency	0.46	0.75
Negative welfare	0.45	0.74
Environmental control	0.37	0.67
Effect of experience	0.31	0.61
Psychological stimulation	0.26	0.55
Stress coping	0.23	0.51
Welfare average	0.45	0.72
SWB Goal achievement	0.74	0.91
SWB Happiness as animal	0.64	0.86
SWB Time animal is happy	0.63	0.85
SWB Social satisfaction	0.51	0.78
SWB Average	0.63	0.85

Note. Based on 48 brown capuchins. Welfare items $k = 3.48$. SWB items $k = 3.33$.

To calculate personality component scores we aggregated HPQ item scores across raters and generated component scores for the personality dimensions based on the 2013 published structure (Table 6 in Morton et al., 2013). This structure includes five brown capuchin personality dimensions: Assertiveness is made up of items such as *bullying*, *aggressive*, and *dominant*; Openness is made up of items such as *inventive*, *innovative*, and *playful*; Neuroticism is made up of items such as (not) *stable*, (not) *predictable*, and *excitable*; Sociability which includes *affectionate*, *friendly*, and (not) *solitary*; Attentiveness is made up of items such as (not) *disorganised*, (not) *unperceptive*, and (not) *thoughtless*.

2.5.3. Pearson correlations

To examine the associations between personality, welfare, and SWB we used Pearson correlations. After standardising the variables we correlated the personality dimensions and the welfare and SWB items and components. We interpreted the results adjusted for multiple tests using a Holm-Bonferroni correction.

2.5.4. Generalizable linear mixed models

We fit linear mixed-effects models using the nlme package (Pinheiro et al., 2012). In all models we included age and sex as fixed effects and facility as a random effect. Our dependent variables were the component scores based on the results of the PCAs of the welfare and SWB items Each of these models included three combinations of fixed effects: 1) locomotor stereotypy frequency; 2) the five capuchin personality dimensions; 3) the five personality dimensions and locomotor stereotypy frequency. Locomotor stereotypy frequency was included in models as the aggregation of stereotypy scores across raters. Housing was not included in our models as only three capuchins were reported to ever be pair-housed, the rest were group housed. The dependent variables were converted into z-scores (mean ± SD = 0 ± 1). The continuous predictor variables (stereotypy, age, and personality dimension) were

Table 2
PCA of brown capuchin welfare items.

Item	Loading	h^2
Positive/negative experience	0.93	0.87
Number of relationships	0.93	0.86
Stress frequency	−0.90	0.81
Negative welfare	−0.84	0.71
Positive welfare	0.84	0.70
Quality of relationships	0.83	0.69
Social control	0.82	0.67
Environmental control	0.80	0.65
Stress coping	0.72	0.52
Psychological stimulation	0.61	0.38
Effect of experience	0.60	0.36
Physical health	0.50	0.25

Note. N = 66. Proportion of variance = 62%. h^2 = commonalities.

centred and divided by 2 × SD to make the effect size comparable with the binary variable (sex) (Gelman, 2008). We then calculated conditional R^2, which gives the variation explained by the fixed and random effects in the model, using the MuMIn package (Barton, 2015).

3. Results

3.1. Items interrater reliabilities

For the welfare items the ICC(3,1) ranged from 0.23 to 0.63 with a mean of 0.45 and the ICC(3,*k*) ranged from 0.51 to 0.86 with a mean of 0.72 (Table 1). For the SWB items the ICC(3,1) ranged from 0.51 to 0.74 with a mean of 0.63 and the ICC(3,*k*) ranged from 0.78 to 0.91 with a mean of 0.85 (Table 1). For the HPQ items the ICC(3,1) ranged from 0.12 to 0.74 with a mean of 0.39 and the ICC(3,*k*) ranged from 0.30 to 0.90 with a mean of 0.64 (S1). For ratings of stereotypic behaviour the ICC(3,1) was 0.64 and ICC(3,*k*) was 0.82 ($k = 2.61$).

3.2. PCA of welfare items and SWB items

A parallel analysis and scree plot of the welfare items showed a single component (Table 2). When we included both the welfare and SWB items in a joint-PCA we again found a single component. All 16 items had salient loadings on this component (Table 3); we named this component welfareSWB.

Table 3
PCA of brown capuchin welfare and subjective well-being items.

Item	Loading	h^2
SWB Happiness as animal	0.93	0.87
Number of relationships	0.93	0.87
SWB Time animal is happy	0.92	0.85
Positive/negative experience	0.92	0.85
Stress frequency	−0.90	0.80
SWB Social satisfaction	0.88	0.78
SWB Goal achievement	0.85	0.73
Social control	0.84	0.71
Quality of relationships	0.83	0.70
Positive welfare	0.83	0.69
Negative welfare	−0.82	0.68
Environmental control	0.76	0.58
Stress coping	0.74	0.54
Effect of experience	0.59	0.35
Psychological stimulation	0.57	0.33
Physical health	0.49	0.24

Note. N = 66. Proportion of variance explained = 66%. h^2 = commonalities.

3.3. Pearson correlations of welfare, SWB, and personality

The welfare component and SWB component were highly correlated ($r = 0.91$, $p < 0.001$, 95% CI 0.86–0.95). Higher Sociability correlated with the higher welfare, higher SWB, and higher welfareSWB scores (Table 4); capuchins rated as more sociable were rated as having better welfare and higher happiness. Assertiveness correlated with the SWB component but not the welfare or welfareSWB components. The full correlation matrix including all items and components is available in Supplementary Table 2.

3.4. Mixed-effects models

3.4.1. Welfare

In the model that included stereotypy but not personality we found that capuchins that performed locomotor stereotypies more frequently were rated as being significantly lower in welfare (Table 5, left panel). In both the model with the five personality dimensions and in the model that included stereotypy frequency, capuchins lower in Neuroticism and higher in Sociability, Assertiveness, and Attentiveness were rated as having significantly better welfare (Table 5, middle and right panels).

Table 4
Pearson correlation coefficients of brown capuchin personality components and welfare and SWB components.

Component	Welfare	95% CI	SWB	95% CI	WelfareSWB	95% CI
Assertiveness	**0.37**	[0.14, 0.56]	**0.49**	[0.28, 0.65]	**0.41**	[0.18, 0.59]
Openness	0.25	[0.01, 0.46]	0.27	[−0.03, 0.48]	0.26	[0.02, 0.47]
Neuroticism	−0.28	[−0.49, -0 −0.05]	−0.24	[−0.46, 0.00]	−0.28	[−0.49, −0.04]
Sociability	**0.72**	[0.58, 0.82]	**0.69**	[0.54, 0.80]	**0.72**	[0.58, 0.82]
Attentiveness	−0.19	[−0.41, 0.05]	−0.22	[−0.44, 0.02]	−0.21	[−0.43, 0.04]

Note. N = 66. Boldface values were significant at p < 0.01. Adjusted for multiple tests.

Table 5
Models of brown capuchin welfare component predicted by stereotypy and personality, controlling for age and sex with facility as a random effect.

Predictor	*b*	CI	p	*b*	CI	p	*b*	CI	p
Intercept	0.18	[−0.22, 0.58]	0.042	0.17	[0.07, 0.42]	0.008	0.16	[−0.06, 0.39]	0.003
Stereotypy	−0.77	[−1.21, −0.33]	**<0.001**	–	–	–	−0.26	[−0.63, 0.10]	0.16
Age	−0.55	[−1.00, −0.10]	**0.018**	−0.58	[−1.00, −0.15]	**0.009**	−0.57	[−0.99, −0.15]	**0.009**
Male	−0.36	[−0.80, 0.08]	0.11	−0.38	[−0.72, −0.04]	**0.031**	−0.35	[−0.69, −0.01]	**0.045**
Sociability	–	–	–	1.21	[0.76, 1.65]	**<0.001**	1.03	[0.54, 1.53]	**<0.001**
Assertiveness	–	–	–	0.56	[0.20, 0.92]	**0.003**	0.56	[0.20, 0.92]	**0.003**
Openness	–	–	–	−0.28	[−0.76, 0.20]	0.23	−0.16	[−0.67, 0.35]	0.53
Neuroticism	–	–	–	−0.55	[−1.03, −0.07]	**0.025**	−0.63	[−1.11, −0.14]	**0.012**
Attentiveness	–	–	–	0.58	[0.16, 1.01]	**0.008**	0.58	[0.16, 1.00]	**0.007**

Note. N = 66. Boldface values were significant at p < 0.05. Variance explained: left panel: $R^2 = 0.31$, middle panel: $R^2 = 0.62$, right panel: $R^2 = 0.62$.

Please cite this article in press as: Robinson, L.M., et al., Happiness is positive welfare in brown capuchins (Sapajus apella). Appl. Anim. Behav. Sci. (2016), http://dx.doi.org/10.1016/j.applanim.2016.05.029

Table 6
Models of brown capuchin SWB component predicted by stereotypy and personality, controlling for age and sex with facility as a random effect.

Predictor	*b*	CI	p	*b*	CI	p	*b*	CI	p
Intercept	0.09	[−0.23,0.40]	0.091	0.10	[−0.18,0.39]	0.10	0.10	[−0.17,0.36]	0.099
Stereotypy	−0.68	[−1.14,0.21]	**0.005**	–	–	–	−0.19	[−0.58,0.19]	0.32
Age	−0.48	[−0.94,−0.01]	**0.046**	−0.40	[−0.85,0.05]	0.079	−0.40	[−0.84,0.05]	0.078
Male	−0.18	[−0.65,0.29]	0.44	−0.24	[−0.59,0.11]	0.18	−0.22	[−0.58,0.14]	0.22
Sociability	–	–	–	1.13	[0.66,1.59]	**<0.001**	0.99	[0.47,1.51]	**<0.001**
Assertiveness	–	–	–	0.79	[0.42,1.16]	**<0.001**	0.79	[041,1.16]	**<0.001**
Openness	–	–	–	−0.23	[−0.72,0.26]	0.35	−0.14	[−0.67,0.39]	0.59
Neuroticism	–	–	–	−0.40	[−0.90,0.10]	0.11	−0.45	[−0.96,0.05]	0.079
Attentiveness	–	–	–	0.44	[−0.01,0.88]	0.056	0.42	[−0.03,0.86]	0.066

Note. N = 66. Boldface values were significant at p < 0.05. Variance explained: left panel: $R^2 = 0.19$, middle panel: $R^2 = 0.60$, right panel: $R^2 = 0.60$.

3.4.2. *SWB*

In the model that included stereotypy but not personality we found that capuchins that performed more stereotypy were rated as having significantly lower SWB (Table 6, left panel). In both the model with the five personality dimensions and the model including the personality dimensions and stereotypy, capuchins with higher Sociability and Assertiveness were rated as having significantly higher SWB (Table 6, middle and right panels). None of the other personality traits were significantly associated with SWB.

3.4.3. *WelfareSWB*

In the model that included stereotypy we found that capuchins who displayed stereotypic behaviour more frequently were rated as being significantly lower in welfareSWB (Table 7, left panel). In the model that included the five personality traits we found that capuchins higher in Sociability, Assertiveness, and Attentiveness and lower in Neuroticism had significantly higher welfareSWB (Table 7, middle panel). Finally, in the model with the five personality dimensions and stereotypy we again found higher Sociability, Assertiveness, and Attentiveness dimensions and lower Neuroticism were significantly related to higher ratings of welfare and SWB (Table 7, right panel).

3.4.4. *Sensitivity test*

We conducted sensitivity tests of the models by removing the 18 capuchins that had been concurrently rated on the welfare, SWB, and HPQ questionnaires. We found some effects were no longer significant. However, the effect sizes were largely similar suggesting that this was due to loss of statistical power. See Supplementary Tables 3–5 for full models.

4. Discussion

We found there was good evidence for staff agreement of ratings of welfare. The welfare items formed a single component. The welfare ratings were correlated with ratings of SWB and formed a single component with SWB items. These results suggest that ratings of SWB and welfare ratings are indistinguishable in brown capuchins. Welfare and SWB ratings were associated with the exhibition of stereotypic behaviour. Finally, four of the five brown capuchin personality dimensions were associated with their welfare, even after adjusting for the presence of locomotor stereotypies. In all models the effect of Sociability and Assertiveness was larger than age, sex, and stereotypy.

These findings suggest that facilities housing animals can make use of the knowledge and experience of their staff to collect additional data on animal welfare. The reliability of ratings were relatively high and on par with reliabilities with those in studies of human personality (Gosling, 2001) and subjective well-being (Diener, 2009). As suggested by other authors, our results demonstrate that staff members are reliable, credible, and valuable sources of welfare data (Meagher, 2009; Whitham and Wielebnowski, 2009). Additionally, the welfare questionnaire was reported to take as little as three minutes showing the utility of questionnaires as a quick addition to traditional assessment methods. In the future we can expand on this research by examining the validity of welfare ratings in other nonhuman primate species.

The welfare items formed a single component suggesting that the aspects of welfare that our questionnaire covered (stress coping, physical health, control, etc.) are connected. Lower welfare and SWB ratings were associated with the higher frequency of stereotypic behaviour. As stereotypy is an abnormal behaviour specific to captivity (Mason, 1991) this suggests that the SWB and welfare questionnaires are measuring an observed welfare state. An alternative explanation may be that raters are familiar with the literature surrounding stereotypy and see it as a negative welfare indicator. Raters who had noted stereotypies were presumably more likely to rate that animal lower in welfare and SWB thus biasing ratings downward. This may be problematic as the literature is mixed regarding the validity of stereotypy as a negative welfare indicator (Mason and Latham, 2004; Mason, 1991). The fact that our stereotypy results validated our welfare and SWB measures still indicates the utility of the measure, but highlights the need for additional metrics that may be less obvious to observers, such as stress hormone levels, to provide further validation.

Sociability had the largest effect on welfareSWB, which fits what we know about the importance of primate sociality. Socially deprived primates are prone to self-injury and are at greater risk

Table 7
Models of brown capuchin welfareSWB component predicted by stereotypy and personality, controlling for age and sex with facility as a random effect.

Predictor	*B*	CI	p	*b*	CI	p	*b*	CI	p
Intercept	0.15	[−0.22,0.53]	0.047	0.15	[−0.10,0.40]	0.015	0.15	[−0.08,0.38]	0.014
Stereotypy	−0.76	[−1.20,−0.31]	**0.001**	–	–	–	−0.25	[−0.62,0.11]	0.17
Age	−0.54	[−1.00,−0.09]	**0.020**	−0.54	[−0.97,−0.12]	**0.013**	−0.54	[−0.96,−0.12]	**0.013**
Male	−0.31	[−0.76,0.14]	0.17	−0.34	[−0.68,−0.00]	**0.048**	−0.32	[−0.65,0.02]	0.070
Sociability	–	–	–	1.19	[0.75,1.63]	**<0.001**	1.02	[0.53,1.51]	**<0.001**
Assertiveness	–	–	–	0.63	[0.28,0.99]	**<0.001**	0.63	[0.28,0.98]	**<0.001**
Openness	–	–	–	−0.24	[−0.73,0.22]	0.28	−0.14	[−0.64,0.36]	0.57
Neuroticism	–	–	–	−0.53	[−1.01,−0.06]	**0.029**	−0.60	[−1.08,−0.13]	**0.014**
Attentiveness	–	–	–	0.55	[0.12,0.97]	**0.013**	0.54	[0.12,0.95]	**0.013**

Note. N = 66. Boldface values were significant at p < 0.05. Variance explained: left panel: $R^2 = 0.28$, middle panel: $R^2 = 0.63$, right panel: $R^2 = 0.63$.

Please cite this article in press as: Robinson, L.M., et al., Happiness is positive welfare in brown capuchins (*Sapajus apella*). Appl. Anim. Behav. Sci. (2016), http://dx.doi.org/10.1016/j.applanim.2016.05.029

of displaying stereotypies (Gottlieb et al., 2013; Lutz et al., 2003). Conversely, primates who create high quality social relationships benefit in terms of their psychological and physical health. For example, they have lower stress levels (Shutt et al., 2007; Terry, 1970) and reduced parasite loads (Akinyi et al., 2013; Crofoot et al., 2011).

We found Assertiveness to have the second largest effect on welfareSWB. The link between Assertiveness and welfare rating may be connected to rank, as a previous study of 38 of these subjects found that Assertiveness and alpha status were associated (Lefevre et al., 2014). Within some primate species high rank confers advantages that may lead to better welfare, including primary access to food (Boccia et al., 1988; Janson, 1985; Wittig and Boesch, 2003) and grooming (Coelho et al., 1983; Leinfelder et al., 2001; Parr et al., 1997), and reduced stress levels (Abbott et al., 2003; Sapolsky, 2004). Thus, it may be the link between Assertiveness and alpha status that creates the positive association with welfare and subjective well-being.

Personality differences have potential real world applications. For example, Capitanio et al. (2015) found that female rhesus macaques with more similar personalities were more likely to be successfully pair-housed. In addition, personality traits are associated with self-injurious behaviour in chimpanzees (Herrelko et al., 2012) and illness duration in golden snub-nosed monkeys (Jin et al., 2013). Our study adds to this literature by demonstrating that certain personality traits are associated with welfare ratings, which can be used to more carefully monitor capuchins with these traits.

There were limitations to our study. We collected data on locomotor stereotypy using questionnaires but we could not assess the effect of type of stereotypy. Furthermore, we did not examine other types of stereotypical behaviour. This may be important as different types of stereotypy (pacing, rocking, oral) may be related to different aspects of welfare. The stereotypy data was also collected a year after the welfare ratings, which may mean that some of the reported stereotypic behaviour may have developed during that time. However, the strong association between welfare and SWB suggest this may not be the case. Additionally, we included stereotypy to check the validity of the welfare questionnaire, but lacked an equivalent positive welfare indicator such as grooming.

The reliability and validity means that this welfare questionnaire, in addition to traditional assessment methods, may be a viable and practical tool. These findings also show that to account for welfare we need to expand our definition to include positive states of subjective well-being or happiness. Finally, this study reaffirms the strong links, identified in other species, including humans, between personality and welfare.

Acknowledgements

First and foremost, we thank the raters for taking the time to fill out the questionnaires. Thank you to Alessia Tosi and Felix Sussenbach for R support. Also thank you to the department heads for approving this project.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.applanim.2016.05.029.

References

Abbott, D., Keverne, E., Bercovitch, F., Shively, C., Mendoza, S., Saltzman, W., Snowdon, C., Ziegler, T., Banjevic, M., Garland, T., Sapolsky, R., 2003. Are subordinates always stressed? A comparative analysis of rank differences in cortisol levels among primates. Horm. Behav. 43, 67–82, http://dx.doi.org/10.1016/S0018-506X(02)00037-5.

Akinyi, M.Y., Tung, J., Jeneby, M., Patel, N.B., Altmann, J., Alberts, S.C., 2013. Role of grooming in reducing tick load in wild baboons (Papio cynocephalus). Anim. Behav. 85, 559–568, http://dx.doi.org/10.1016/j.anbehav.2012.12.012.

Barton, K., 2015. MuMIn: Multi-model inference R package version 1.9.13. Version 1, 18. citeulike:11961261.

Boccia, M.L., Laudenslager, M., Reite, M.L., 1988. Food distribution, dominance, and aggressive behaviors in bonnet macaques. Am. J. Primatol. 16, 123–130, http://dx.doi.org/10.1002/ajp.1350160203.

Boissy, A., Manteuffel, G., Jensen, M.B., Moe, R.O., Spruijt, B., Keeling, L.J., Winckler, C., Forkman, B., Dimitrov, I., Langbein, J., Bakken, M., Veissier, I., Aubert, A., 2007. Assessment of positive emotions in animals to improve their welfare. Physiol. Behav. 92, 375–397, http://dx.doi.org/10.1016/j.physbeh.2007.02.003.

Broom, D.M., Johnson, K.G., 1993. Stress and animal welfare. In: Animal Welfare. Chapman and Hall, London.

Broom, D.M., 1988. The scientific assessment of animal welfare. Appl. Anim. Behav. Sci. 20, 5–19, http://dx.doi.org/10.1016/0168-1591(88)90122-0.

Broom, D.M., 1991. Animal welfare: concepts and measurement. J. Anim. Sci. 69, 4167–4175 https://dl.sciencesocieties.org/publications/jas/abstracts/69/10/4167.

Broom, D.M., 2006. Behaviour and welfare in relation to pathology. Appl. Anim. Behav. Sci. 97, 73–83, http://dx.doi.org/10.1016/j.applanim.2005.11.019.

Broom, D.M., 2007. Quality of life means welfare: how is it related to other concepts and assessed? Anim. Welf. 16, 45–53.

Capitanio, J.P., Blozis, S., Snarr, J., Steward, A., McCowan, B., 2015. Do birds of a feather flock together or do opposites attract? Behavioral responses and temperament predict success in pairings of rhesus monkeys in a laboratory setting. Am. J. Primatol., 1–11, http://dx.doi.org/10.1002/ajp.22464.

Coelho Jr., A.M., Turner, S.A., Bramblett, C.A., 1983. Allogrooming and social status: an assessment of the contributions of female behavior to the social organization of hamadryas baboons (Papio hamadryas). Primates 24, 184–197, http://dx.doi.org/10.1007/BF02381081.

Cohen, S., Kaplan, J., Cunnick, J.E., Manuck, S.B., Rabin, B.S., 1992. Chronic social stress, fffiliation, and cellular immune response in nonhuman primates. Psychol. Sci. 3, 301–304, http://dx.doi.org/10.1111/j.1467-9280.1992.tb00677.x.

Crofoot, M.C., Rubenstein, D.I., Maiya, A.S., Berger-Wolf, T.Y., 2011. Aggression, grooming and group-level cooperation in white-faced capuchins (Cebus capucinus): insights from social networks. Am. J. Primatol. 73, 821–833, http://dx.doi.org/10.1002/ajp.20959.

Davenport, M.D., Lutz, C.K., Tiefenbacher, S., Novak, M.A., Meyer, J.S., 2008. A rhesus monkey model of self-Injury: effects of relocation stress on behavior and neuroendocrine function. Biol. Psychiatry 63, 990–996, http://dx.doi.org/10.1016/j.biopsych.2007.10.025.

Diener, E., Chan, M.Y., 2011. Happy people live longer: subjective well-being contributes to health and longevity. Appl. Psychol. Health Well-Being 3, 1–43, http://dx.doi.org/10.1111/j.1758-0854.2010.01045.x.

Diener, E., Oishi, S., Lucas, R.E., 2003. Personality, culture, and subjective well-being: emotional and cognitive evaluations of life. Annu. Rev. Psychol. 54, 403–425, http://dx.doi.org/10.1146/annurev.psych.54.101601.145056.

Diener, E., 2009. Subjective well-being, in: The Science of Well-Being: The Collected Works of Diener. Springer, pp. 11–58, http://dx.doi.org/10.1007/978-90-481-2350-6.

Dinno, A., and Dinno, M., 2010. R package paran.

Downey, R.G., King, C., 1998. Missing data in Likert ratings: a comparison of replacement methods. J. Gen. Psychol. 125, 175–191, http://dx.doi.org/10.1080/00221309809595542.

Fragaszy, D.M., Visalberghi, E., Fedigan, L.M., 2004. The Complete Capuchin: The Biology of the Genus Cebus. Reading, http://dx.doi.org/10.1007/s10329-005-0129-9.

Gartner, M.C., Weiss, A., 2013. Scottish wildcat (Felis silvestris grampia) personality and subjective well-being: implications for captive management. Appl. Anim. Behav. Sci. 147, 261–267, http://dx.doi.org/10.1016/j.applanim.2012.11.002.

Gelman, A., 2008. Scaling regression inputs by dividing by two standard deviations. Stat. Med. 27, 2865–2873, http://dx.doi.org/10.1002/sim.3107.

Gorsuch, R.L., 1983. Factor Analysis, 2nd ed. Erlbaum Hillsdale, NJ.

Gosling, S.D., 2001. From mice to men: what can we learn about personality from animal research? Psychol. Bull. 127, 45–86, http://dx.doi.org/10.1037/0033-2909.127.1.45.

Gottlieb, D.H., Capitanio, J.P., Mccowan, B., 2013. Risk factors for stereotypic behavior and self-biting in rhesus macaques (Macaca mulatta): animal's history, current environment, and personality. Am. J. Primatol. 75, 995–1008, http://dx.doi.org/10.1002/ajp.22161.

Green, T.C., Mellor, D.J., 2011. Extending ideas about animal welfare assessment to include quality of life and related concepts. N. Z. Vet. J. 59, 263–271, http://dx.doi.org/10.1080/00480169.2011.610283.

Herrelko, E.S., Vick, S.J., Buchanan-Smith, H.M., 2012. Cognitive research in zoo-housed chimpanzees: influence of personality and impact on welfare. Am. J. Primatol. 74, 828–840, http://dx.doi.org/10.1002/ajp.22036.

Horn, J.L., 1965. A rationale and test for the number of factors in factor analysis. Psychometrika 30, 179–185, http://dx.doi.org/10.1007/BF02289447.

IUCN, 2014. IUCN Red List of Threatened Species [WWW Document] Version 2013.1, URL www.iucnredlist.org.

Janson, C.H., 1985. Aggresive competition and individual food consumption in wild brown capuchin monkeys (Cebus apella). Behav. Ecol. Sociobiol. 18, 125–138, http://dx.doi.org/10.1007/BF00299041.

Jin, J., Su, Y., Tao, Y., Guo, S., Yu, Z., 2013. Personality as a predictor of general health in captive golden snub-nosed monkeys (Rhinopithecus roxellana). Am. J. Primatol. 75, 524–533, http://dx.doi.org/10.1002/ajp.22127.

King, J.E., Landau, V.I., 2003. Can chimpanzee (Pan troglodytes) happiness be estimated by human raters? J. Res. Pers. 37, 1–15, http://dx.doi.org/10.1016/S0092-6566(02)00527-5.

Laule, G.E., Bloomsmith, M. a., Schapiro, S.J., 2003. The use of positive reinforcement training techniques to enhance the care, management, and welfare of primates in the laboratory. J. Appl. Anim. Welf. Sci. 6, 163–173, http://dx.doi.org/10.1207/S15327604JAWS0603_02.

Lefevre, C.E., Wilson, V.A.D., Morton, F., Brosnan, S.F., Paukner, A., Bates, T.C., 2014. Facial width-to-height ratio relates to alpha status and assertive personality in capuchin monkeys. PLoS One 9, http://dx.doi.org/10.1371/journal.pone.0093369.

Leinfelder, I., de Vries, M., Deleu, R., Nelissen, M., 2001. Rank and grooming reciprocity among females in a mixed-sex group of captive hamadryas baboons. Am. J. Primatol. 55, 25–42, http://dx.doi.org/10.1002/ajp.1036.

Lutz, C.K., Well, A., Novak, M. a., 2003. Stereotypic and self-injurious behavior in rhesus macaques: a survey and retrospective analysis of environment and early experience. Am. J. Primatol. 60, 01–15, http://dx.doi.org/10.1002/ajp.10075.

Mason, G.J., Latham, N.R., 2004. Can't stop, won't stop: is stereotypy a reliable animal welfare indicator? Anim. Welf. 13, S57–S70.

Mason, G.J., 1991. Stereotypies: a critical review. Anim. Behav. 41 (6), 1015–1037.

McMillan, F., 2005. Mental wellness: the concept of quality of life in animals Mental Health and Well-Being in Animals. Blackwell publishing.

Meagher, R.K., 2009. Observer ratings: validity and value as a tool for animal welfare research. Appl. Anim. Behav. Sci. 119, 1–14, http://dx.doi.org/10.1016/j.applanim.2009.02.026.

Morton, F., Lee, P.C., Buchanan-Smith, H.M., Brosnan, S.F., Thierry, B., Paukner, A., de Waal, F.B.M., Widness, J., Essler, J.L., Weiss, A., 2013. Personality structure in brown capuchin monkeys (Sapajus apella): comparisons with chimpanzees (Pan troglodytes), orangutans (Pongo spp.), and rhesus macaques (Macaca mulatta). J. Comp. Psychol. 127, 282–298, http://dx.doi.org/10.1037/a0031723.

Parr, L., Matheson, M., Bernstein, I., de Waal, F.B.M., 1997. Grooming down the hierarchy: allogrooming in captive brown capuchin monkeys, Cebus apella. Anim. Behav. 54, 361–367, http://dx.doi.org/10.1006/anbe.1996.0419.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Development Core Team, 2012. nlme: Linear and Nonlinear Mixed Effects Models. October.

R Development Core Team, 2014. R A Lang Environ. Stat. Comput.

Rushen, J., 1991. Problems associated with the interpretation of physiological data in the assessment of animal welfare. Appl. Anim. Behav. Sci. 28 (4), 381–386, http://dx.doi.org/10.1016/0168-1591(91)90170-3.

Sandvik, E., Diener, E., Seidlitz, L., 1993. Subjective well-being—the convergence and stability of self-report and non-self-report measures. J. Pers. 61, 318–342, http://dx.doi.org/10.1111/j.1467-6494.1993.tb00283.x.

Sapolsky, R.M., 2004. Social status and health in humans and other animals. Annu. Rev. Anthropol. 33, 393–418, http://dx.doi.org/10.1146/annurev.anthro.33.070203.144000.

Shrout, P.E., Fleiss, J.L., 1979. Intraclass correlations: uses in assessing rater reliability. Psychol. Bull. 86, 420–428, http://dx.doi.org/10.1037/0033-2909.86.2.420.

Shutt, K., MacLarnon, A., Heistermann, M., Semple, S., 2007. Grooming in Barbary macaques: better to give than to receive? Biol. Lett. 3, 231–233, http://dx.doi.org/10.1098/rsbl.2007.0052.

Terry, R.L., 1970. Primate grooming as a tension reduction mechanism. J. Psychol. 76, 129–136, http://dx.doi.org/10.1080/00223980.1970.9916830.

Tetley, C.L., O'Hara, S.J., 2012. Ratings of animal personality as a tool for improving the breeding, management and welfare of zoo mammals. Anim. Welf. 21, 463–476, http://dx.doi.org/10.7120/09627286.21.4.463.

USDA, 2008. Animal Welfare Act.

Vandeleest, J.J., McCowan, B., Capitanio, J.P., 2011. Early rearing interacts with temperament and housing to influence the risk for motor stereotypy in rhesus monkeys (Macaca mulatta). Appl. Anim. Behav. Sci. 132, 81–89, http://dx.doi.org/10.1016/j.applanim.2011.02.010.

Vazire, S., Gosling, S.D. Dickey, A.S., Schapiro, S.J., 2007. Measuring personality in nonhuman animals Handbook of Research Methods in Personality Psychology 2007; 190-206 10.1002/zoo.20379.

Weiss, A., King, J.E., Perkins, L., 2006. Personality and subjective well-being in orangutans (Pongo pygmaeus and Pongo abelii). J. Pers. Soc. Psychol. 90, 501–511, http://dx.doi.org/10.1037/0022-3514.90.3.501.

Weiss, A., Inoue-Murayama, M., Hong, K.W., Inoue, E., Udono, T., Ochiai, T., Matsuzawa, T., Hirata, S., King, J.E., 2009. Assessing chimpanzee personality and subjective well-being in japan. Am. J. Primatol. 71, 283–292, http://dx.doi.org/10.1002/ajp.20649.

Weiss, A., Adams, M.J., King, J.E., 2011a. Happy orang-utans live longer lives. Biol. Lett. 7, 872–874, http://dx.doi.org/10.1098/rsbl.2011.0543.

Weiss, A., Adams, M.J., Widdig, A., Gerald, M.S., 2011b. Rhesus macaques (Macaca mulatta) as living fossils of hominoid personality and subjective well-being. J. Comp. Psychol. 125, 72–83, http://dx.doi.org/10.1037/a0021187.

Whitham, J.C., Wielebnowski, N., 2009. Animal-based welfare monitoring: using keeper ratings as an assessment tool. Zoo Biol. 28, 545–560, http://dx.doi.org/10.1002/zoo.20281.

Wittig, R.M., Boesch, C., 2003. Food competition and linear dominance hierarchy among female chimpanzees of the Taı National Park. Int. J. Primatol. 24, 847–867.

Yeates, J.W., Main, D.C.J., 2008. Assessment of positive welfare: a review. Vet. J. 175, 293–300.

Please cite this article in press as: Robinson, L.M., et al., Happiness is positive welfare in brown capuchins (*Sapajus apella*). Appl. Anim. Behav. Sci. (2016), http://dx.doi.org/10.1016/j.applanim.2016.05.029