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The Behavioural Ecology of Personality in Wild Barbary Macaques

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The Behavioural Ecology of Personality in Wild Barbary Macaques

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“A personality is the product of a clash between two opposing forces: the urge to create a life of one's own and the insistence by the world around us that we conform.”

Hermann Hesse

Soul of the Age: Selected Letters, 1891-1962

Abstract

Personality, that is intra-individual consistency and inter-individual variation in behaviour, is widespread throughout the animal kingdom. This challenges traditional evolutionary assumptions that selection should favour behavioural flexibility, and that variation in behavioural strategies reflects stochastic variation around a single optimal behavioural strategy. Adaptive models to explain personality within the framework of evolutionary and behavioural ecology exist, and are typically empirically explored by identifying proximate associations to, and the functional consequences of, personality expression. To date, such studies have typically quantified a narrow range of personality traits within a species, and focused on captive populations or species with relatively limited behavioural or social repertoires. In this thesis, personality is studied in wild Barbary macaques (*Macaca sylvanus*). Quantification of personality structure in the species was conducted using a multi-method approach, and subsequently, it was examined whether physiological stress response (a proximate association) was related to personality expression, and whether personality expression affected social (functional) outcomes for individuals. Seven personality constructs were identified in Barbary macaques. Three personality constructs were related to physiological stress responses (Excitability, Tactility and Exploration), with the relationship between stress and personality expression dependent on sex, and in some cases rank or age. Two personality constructs (Excitability and Exploration) were associated with measures of social integration. Subjects generally socially assorted themselves according to personality, tending to be in proximity to individuals with a similar personality to themselves. This study contributes methodologically by

demonstrating the plausibility of multi-method approaches to measuring personality in wild primates, and empirically, by generating evidence supporting adaptive models for the evolution of personality, namely that intra-individual consistency in behaviour may be mediated by physiology and that inter-individual variation in behaviour has functional benefits in the formation of social relationships and social structures.

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1| Introduction

Personality, that is inter-individual variation and intra-individual consistency in behaviour, has now been found in a wide range of animal taxa, provoking interest in the causes, consequences and evolutionary history of personality (Réale et al, 2007; Wolf & Weissing, 2010; Wolf & Weissing, 2012). Until recently, personality research has largely been the domain of human psychology. However, the practical challenges of collecting long-term, objective data in human subjects has limited the scope of research, particularly in terms of exploring adaptive models for the evolution of personality (Mehta & Gosling, 2008). Group-living, non-human primates (hereafter primates) experience complex social worlds characterised by a broad range of social interactions and diverse and differentiated social relationships (Smuts et al, 1987). These animals also share many of the human anatomical structures and physiological processes which may give rise to, or be associated with, personality expression (Chang et al, 2013). Given our ancestral links, non-human primate research provides exciting opportunities to integrate mechanistic and functional approaches to improve not only our understanding of human personality and social functioning, but also our understanding of how personality shapes and is shaped by factors such as endocrinology and sociality in a broader range of animal species than presently exist within the literature. In this thesis, a multi-method approach is used to quantify personality in wild non-human primate population. The relationship between personality and physiological stress response and sociality is then examined in detail using non-invasive endocrinology and social network analyses.

1.1 The Concept of Personality

Personality can colloquially be defined as the sum of the behavioural characteristics that differentiate one individual from another. However, this is a vague definition and developing a concrete, working classification has been a struggle for psychologists. One of the first textbooks on human personality, Allport's "Personality: A psychological interpretation" (1937), listed 49 different definitions of personality (McAdams & Pals, 2006). This created considerable challenges to developing a method for comparing variation in "personality" between individuals. Psychologists overcame this by compartmentalising human personality into "constructs" (Wiggins, 1973). Within this framework, personality constructs became defined as "broad dimensions of psychological individuality that describe assumedly internal, stable, and global individual differences in behaviour, thought, and feeling" (McAdams & Pals, 2006). On a behavioural level, these constructs of personality may be composed of and expressed via individual traits, such as aggression or risk-taking (Carter et al 2013).

Early personality psychologists used the "Lexical Hypothesis" (Capara, 2000) to categorise constructs of personality in humans. This approach collected adjectives believed to pertain to personality from the dictionary. Clusters of closely-related terms were collated, reducing the list of adjectives down to sixteen broad constructs, from which it was suggested that human personality can be described by a "sixteen factor model" (Cattel, 1957). From this model, one of the first instruments to empirically quantify personality in humans was developed. The "Sixteen Personality Factor Questionnaire" is a self-reporting test in which individuals answer multiple-choice questions, with their responses used to determine scores for sixteen personality categories, examples of which include “sensitivity”, “vigilance” and “stability” (Cattel, 1957).

Subsequently within psychology, there has been a continual debate about the number of, and definitions for, constructs that make up human personality (Eysenck, 1992). Arguably, the most famous conceptualisation of human personality is “The Big Five”, which suggests that all humans have personalities which can be characterised by how much they express five broad personality constructs: openness to experience, conscientiousness, extraversion, agreeableness and neuroticism (Digman, 1990). Each bipolar construct comprises of a range of traits, for example agreeableness includes facets ranging from “cooperation” to “antagonism” (McCrae & Costa, 1987). The number and nature of the constructs of human personality is contentious, and even the notion of dividing personality in this way is not universally accepted within psychology (Gray, 1981). Yet, on a practical level, this concept has allowed researchers to develop self-reporting, five construct-based questionnaires to quantify personality in individuals and it remains one of the most widely-used paradigms in human personality assessment (Thalmayer et al, 2011).

An alternative concept of personality, and how to quantify it, is the “Biopsychological Theory” of personality, later incorporated and reframed into the “Reinforcement Sensitivity Theory” of personality (Corr et al, 1995). It proposes that personality is a reactive disposition that must be investigated in relation to neurological and endocrine processes (reviewed in Corr, 2004). The theory postulates there are three components of reactivity, each controlled by particular neuroendocrine systems: the “flight-or-fight system”, which mediates responses to aversive stimuli; the “behavioural activation system”, which mediates responses to positive stimuli, and the “behavioural inhibition system”, which mediates responses to uncertain or novel stimuli (Gray & McNaughton, 2000). Within psychology literature, this association between personality and proximate processes often leads researchers to prefer the term "temperament" rather than personality (Réale et al, 2007). Here, personality/temperament is conceptualised as an underlying and constant disposition to behave in a particular way, which is a product of genetic, anatomical and physiological traits, such as neuroendocrinology (Strelau, 1998; Réale et al, 2007).

Regardless of how researchers have chosen to conceptualise or quantify personality, that we all have independent natures and are psychologically unique is a central feature of human identity. Therefore, any notion that non-human animals (hereafter animals) may also have individual personalities has been resisted within science for fear of either committing the "sin of anthropomorphism" or worse, being branded as "overly sentimental dog owners" (Gosling & John, 1999; Pennisi, 2016). Despite such prejudices, studies revealing patterns of behavioural consistency and temperament in animals date back to the 1930s and researchers have now identified personality throughout the animal kingdom, including in mammals, birds, fish, arthropods and molluscs (reviewed in Sih et al, 2004; Réale et al, 2007; Gosling & Harley, 2009). Within animal behaviour, the preferred definition for personality is "intra-individual consistency and inter-individual variation in behaviour" (Réale et al, 2007). For example, dumpling squid (*Euprymna tasmanica*) vary in their responses to predators, with some individuals confronting predators, while others flee immediately (Sinn et al, 2006). Furthermore, individual squid are consistent in these responses, i.e. those that are quick to flee, consistently are the quickest to take flight. In tangled web spiders (*Anelosimus studiosus*), certain individuals are consistently aggressive to conspecifics, prey and predators across time and context, while other individuals are consistently docile (Wright et al, 2014). In chimpanzees (*Pan troglodytes*), some individuals have "persistent" personalities, and will explore puzzle boxes and novel objects to receive rewards, while other individuals are consistent in their tendency to rapidly discard such items after a cursory investigation (Massen et al, 2013). Within the field of animal behaviour, rather than use the term personality, many studies refer to these correlations of behavioural traits over time and context as "behavioural syndromes", although nomenclature can be inconsistent and confusing (Carter et al, 2013). To clarify terminology to be used throughout this thesis, table 1.1 provides a glossary of personality-associated terms.

Essentially, personality implies that individuals, human or animal, tend to behave consistently and differently (and consistently differently) from their conspecifics. This is illustrated in figure 1.1 via a "Reaction Norm Plot" (Dingemanse & Wolf, 2010). For behavioural and evolutionary ecologists this generates two key questions (Réale et al, 2007; Dingemanse & Wolf, 2010; Wolf & Weissing, 2010; Wolf & Weissing, 2012): Why are individuals not completely flexible in their behavioural repertoires? How and why do several behavioural phenotypes coexist within a population or species?

Table 1.1: Glossary of common terms used within personality research.

Term	Definition
Personality	Intra-individual consistency and inter-individual variation in behaviour across time and/or context (Réale et al, 2007).
Construct	A conceptual component of an individual’s overall personality which is quantifiable and comparable between individuals; i.e. a trait, behavioural syndrome or dimension (see below).
Trait	Broadly within biology, any quantifiable phenotypic characteristic (Massen et al, 2013); in this project, a personality trait is an irreducible personality construct, expressed through particular behaviours and constituent of a larger construct, such as a behavioural syndrome or dimension.
Behavioural syndrome	Two or more behavioural traits correlated over time and context (Carter et al, 2013).
Dimension	Personality construct containing commonly correlated traits that is, ideally, orthogonal to other dimensions (Carter et al, 2013). These are generated using data reduction statistics and thus are either components or factors.

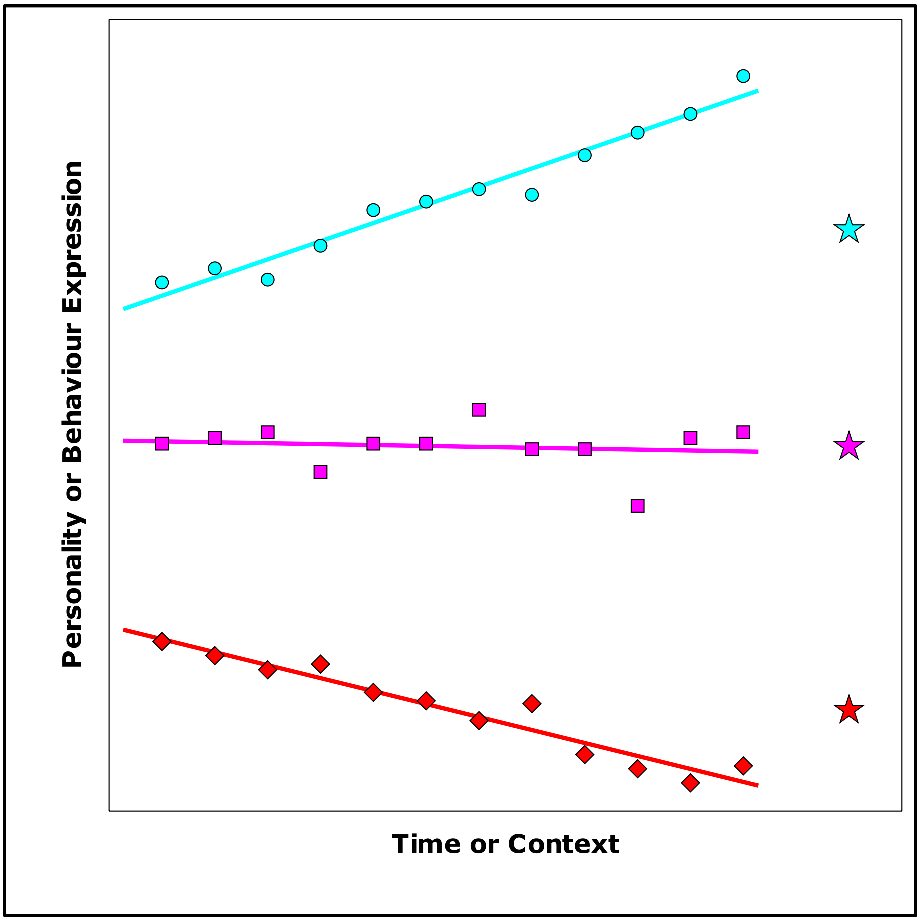


Figure 1.1: "Reaction Norm Plot", adopted from Dingemanse & Wolf (2010). Here, each individual is represented by a series of plots and regression line, with different colours and symbol for each individual. The stars represent average values for individuals. Each individual demonstrates some degree of intra-individual consistency in personality/behaviour expression over time and context (although the degree of consistency varies between the individuals). Individuals also vary in their average expression (represented by stars) of personality/behaviour.

1.2 Adaptive Models for the Origin and Maintenance of Personality

According to traditional evolutionary assumptions, selection should favour behavioural flexibility so that individuals can rapidly adjust to changing situations and environments (West-Eberhard, 1989; Wilson et al, 1994; West-Eberhard, 2003). Personality is defined as intra-individual consistency and inter-individual variation in behavioural repertoires (Réale et al, 2007; Carter et al, 2013). Such behavioural consistency may represent a constraint on behavioural flexibility, which seems potentially maladaptive (West-Eberhard, 1989; Wilson et al, 1994; West-Eberhard, 2003). Maladaptive consequences of behavioural consistency have been demonstrated in a famous example with fishing spiders (*Dolmodes triton*): aggressive spiders are more successful at catching prey than timid spiders; however, this aggression is also directed to conspecifics and, in females, lowers reproductive success as highly aggressive females may cannibalise males prior to copulation (Johnson & Sih, 2005). In humans, personality can sometimes represent a constraint on behavioural flexibility for individuals, manifesting in personality-related disorders where behavioural patterns are difficult to change even when they have immediate negative effects (Costa & McCrae, 1992).

Exploring inter-individual variation in behaviour is also a relatively novel paradigm within the study of behaviour. Following Tinbergen, ethology is usually approached from four perspectives: immediate factors, ontogenetic development, adaptive function and evolutionary history (Tinbergen, 1963). This framework, rooted in evolutionary reasoning, often focuses on understanding optimal evolutionary strategies, with variation around these optima considered as "noise" (Carter et al, 2013; Weiss & Adams, 2013). Within each of

Tinbergen’s ethological perspectives, interest has shifted from understanding the evolution of population means to addressing the evolution of this “noise” and hence closer examination of individual variation (Wilson et al, 1994).

In the last decade, evolutionary theory pertaining to behaviour has had to develop models to explain how behavioural inflexibility or personality may be adaptive and the selective pressures which may maintain variation between individuals, rather than convergence, in behavioural tendencies (Wolf & Weissing, 2010). There are two principal adaptive models which aim to explain how personality may arise and be maintained in a population or species, the first of which is based on frequency-dependent selection (Dall et al, 2004). Frequency-dependent models are based on evolutionary game theory whereby the fitness benefits of a particular strategy depend on the frequency of that strategy and other strategies within a population (Maynard Smith, 1982). Such a paradigm explains why several behavioural phenotypes can exist within a population, but it does not address why these phenotypes remain consistent over time and context. Indeed, frequency-dependent models suggest an advantage to being able to change strategy depending on fluctuations in the frequencies of strategies. Tufto (2000) demonstrated in a mathematical model that being behaviourally or strategically flexible is costly in terms of information gathering and decision making processes. Further, in their review of the evolutionary ecology of personality, Dall et al (2004) suggest behavioural consistency can be selected for when consistency aids cooperation or cohesion within a group. In another mathematical model, Fishman (2003) demonstrated that individuals must be selective in choosing cooperative partners and successful cooperation is more likely if individuals have reliable information on partners, which is possible if individuals are consistent in their cooperative behaviour. In this way, consistent personality expression could function as a social signal (Wolf & Weissing, 2010); for example, Godin & Dugatkin (1996) found that in male Trinidadian guppies (*Poecilia reticulate*), boldness towards predators indicates to conspecifics that these individuals will also be "bold" in any intra-specific aggression or competition.

The second major framework proposed for explaining personality is "state-dependence". Here, an individual's state is defined as any trait, or sum of traits, which affects the cost/benefit trade-off of "behavioural decisions (taken) in order to increase fitness" (Houston & McNamara, 1999; Wolf & Weissing, 2010). Variables which constitute an individual's state include physical characteristics such as body size, health, metabolism, and non-physical factors linked to the individual, such as territory size (Dall et al, 2004). The state-dependent hypothesis for the evolution and maintenance of personality posits that inter-individual variation in behavioural repertoires arises from inter-individual variation in state and that the relative stability of these states within an individual can be related to consistency of behaviour (Biro & Stamps, 2008). For example, a mathematical model using body size as the personality-associated state demonstrated that larger individuals tend to be aggressive compared to smaller individuals as they are capable of outcompeting competitors or repelling predators (Luttbeg & Sih, 2010). A number of candidate states, namely body size, health and metabolic rate, have been empirically linked to variation in personality in some species. In house mice (*Mus musculus*), larger individuals are consistently more explorative in mazes than smaller individuals (Wirth-Dzięciolowska et al, 2005). In Siberian chipmunks (*Tamias sibiricus*), individuals which were consistently less fearful during handling and more explorative in novel cages had higher parasite loads than conspecifics which froze when handled or placed in novel cages (Boyer et al, 2010). In a meta-analysis of research on muroid rodents, basal metabolic rate was negatively correlated with exploratory behaviour (Careau et al, 2009).

Evidence of state leading to personality merely shifts the terms of the original questions, i.e. we must now ask why individuals vary in state and why do several states coexist within a population or species (Wolf & Weissing, 2010)? Beyond stochastic variation, one adaptive framework to explain inter-individual variation in state has been life history strategy. Here, variation in state could arise from the variation in the evolutionary trade-offs individuals experience throughout different life stages (Réale et al, 2010). At different stages of life history, individuals will vary in the degree to which survival or reproduction will be prioritised and this in turn leads to variation in physiological or behavioural traits (Hall et al, 2015). For example, in a simplified example of a trade-off between growth and mortality, younger individuals should prioritise growth, leading to higher energy demands or metabolic rates, which in turn may be associated with young individuals being more explorative in the search for resources. Adults may be larger and more conspicuous to predators, leading them to avoid risks and behave conservatively.

Empirical data now exist to support the link between life history and personality. In Eastern mosquitofish (*Gambusia holbrooki*), smaller, less fecund individuals were more explorative than larger, fecund conspecifics (Wilson et al, 2010). In male bighorn sheep (*Ovis canadensis*), the effect of boldness (quantified based on reactions to human handlers) on reproductive success varied with the age of the subject; in younger rams, boldness had a weak negative effect on reproductive success, whereas in older rams a strong positive effect of boldness on reproductive success was observed (Réale et al, 2009).

Animal personality literature is rich in theoretical work, but there have been calls within behavioural and evolutionary ecology to generate more empirical data to examine these models for the evolution and maintenance of personality (Réale et al, 2007; DiRienzo and Montiligo, 2015). All the empirical studies mentioned so far have focused on quantifying "boldness" or "exploration" as personality traits in animals, yet human personality is considered multi-faceted and multi-dimensional (Digman, 1990; Eysenck, 1992). A number of methods now exist for researchers to comprehensively explore the complexity of personality in their chosen species.

1.3 Quantifying Personality in Animals

The most commonly studied personality construct in animals is "boldness", referring to responses to risky but non-novel situations (Réale et al, 2007), which can be characterised by a number of individual behaviours, such as aggressive, non-fearful or explorative responses to a predator or other dangerous stimuli (Wilson et al, 1994; Wilson & Godin, 2009; Edelaar et al, 2012). The other common focus for animal personality research is "exploration", which refers to responses to novel situations, objects, foods or environments (Réale et al, 2007; Carter et al, 2012). In some species, such as cichlid fish (*Amatitlania siquia*), bold individuals also tend to be explorative (Mazué et al, 2015). In other species, such as Iberian lizards (*Podarcis hispanica*; Rodríguez-Prieto et al, 2011) and chacma baboons (*Papio ursinus*; Carter et al, 2012), boldness and exploration are distinct, non-correlated personality constructs composed of different correlated behaviours. Both "boldness" and "exploration" are typically quantified using experimental asssays, i.e. presenting subjects with stimuli to induce personality-associated behaviours. In some studies, the aforementioned distinction between boldness and exploration is not explored. For example, “boldness” has been experimentally assayed using exploration of open areas (Brown & Braithwaite, 2004), reactions to predators (Watanabe et al, 2012) and reactions to novel objects (Pronk et al, 2010). Using experimental approaches, the researcher is required to predetermine and define the personality of interest in advance. This can give rise to what psychologists have called “jingle-jangle” fallacies, whereby researchers use one term for what are in effect multiple traits (a “jingle” fallacy), or multiple terms for one trait (a “jangle” fallacy; Block, 1995; Carter et al, 2013).

An alternative way to characterise animal personality and avoid these fallacies is to take a “bottom-up” approach by looking at correlations in behaviour across the whole behavioural repertoire of a species or population in a non-experimental setting in order to identify broad components of behavioural consistency (Vazire et al, 2007). For example, behavioural observations of wild chacma baboons revealed three personality constructs in the species, “Aloof”, “Nice” and “Loner”, each with constituent behavioural traits (e.g. aloof baboons were more aggressive and tended not to greet conspecifics with vocalisations; Seyfarth et al, 2012). A “top-down” quantification of personality may also be used in animals by co-opting the questionnaire-based methods used in humans. In humans, subjects complete the questionnaires themselves; in animals, observers and researchers subjectively assess the degree to which subjects express predetermined personality traits, after which correlations among these traits are identified in order to develop broader dimensions of personality (Weiss et al, 2009). For example, subjective assessments of captive cheetahs (*Acinonyx jubatus*) found three dimensions of personality in the species, “tense-fearful”, “excitable-vocal” and “aggressive” (Wielebnowski, 1999).

As with experimental assays, both “bottom-up” and “top-down” approaches to quantifying personality are problematic when used in isolation (Freeman et al, 2013). Collecting enough behavioural data to demonstrate individual differences in behavioural consistency over time and context requires long-term data collection, while trait assessments are inherently subjective (Garai et al, 2016). A further issue with trait assessments is that the development of questionnaires has frequently used the human “Big Five” model of personality as an initial frame of reference, therefore leaving the method open to criticisms of anthropomorphism (Gosling & John, 1999; Konec̆ná et al, 2012). Increasingly, researchers recognise that singular approaches to quantifying personality are insufficient and that multi-method approaches have the advantage of generating a more complete characterisation of personality in a species and generating personality constructs that are more readily cross-species and cross-study comparable (Uher, 2008; Freeman et al, 2013; Iwanicki & Lehmann, 2015; Garai et al, 2016).

Across all methodologies for assessing animal personality, there exists a general paucity of studies in wild animals (Archard & Braithwaite, 2010). As highlighted above, a major focus of personality research is trying to understand the evolutionary ecology of personality, i.e. understanding how intra-individual consistency and inter-individual variation in behavioural traits are maintained (Dingemanse & Reale, 2005; Wolf & Weissing, 2010). Captivity can create animal populations with characteristics distinct from conspecifics found in the wild and facing selective pressures which relate more to husbandry techniques than the selective pressures which have occurred during the species’ evolutionary history (Stockwell et al, 2003; McDougall et al, 2006; Wolfensohn & Honess, 2008).

Therefore, there are two methodological challenges for animal personality researchers: developing a cross-species comparable characterisation of personality for the study species; and studying the species in the wild where selective pressures can be accurately explored. The first results chapter of this thesis (chapter 3) addresses these challenges by utilising and critiquing all three methods (experimental assays, behavioural observations and questionnaire-based trait assessments) to quantify personality in a wild primate species, the Barbary macaque (*Macaca sylvanus*).

Primates generally live in complex, hierarchical social environments composed of kin and non-kin (as is the case with Barbary macaques) and they share with humans a highly complex neurophysiology, which varies in its functioning between individuals (Chang et al, 2013). This makes them useful study species for advancing our understanding of personality because testing the aforementioned adaptive models for the evolution of personality principally requires two approaches: "mechanistic" approaches, which aim to understand how particular phenotypes result from states or proximate factors such as genetics, physiology and environmental factors; and "functional" approaches, which seek to examine how different personality types interact with their environment and the potential fitness outcomes of these interactions (Dingemanse & Réale, 2005).

1.4 Mechanistic Associations of Personality

The heritability of personality has been at the heart of the "nature versus nurture" debate within human psychology for several decades, with research suggesting that an interaction between genes and environment shapes human personality phenotypes (Krueger et al, 2008). Animal studies have also found evidence for the heritability of personality, including in great tits (*Parus major*; Dingemanse et al, 2002; van Oers et al, 2004), dumpling squid (Sinn et al, 2006), chimpanzees (Weiss et al, 2000), vervet monkeys (*Chlorocebus aethiops*; Fairbanks et al, 2004) and rhesus macaques (*Macaca mulatta*; Brent et al, 2013a). The translation of genes into behaviour, and thus personality expression, requires a further mechanistic link. Hormones are communicative intermediaries between organs and tissues mediating gene transcription activity and influencing responses to, and being influenced by, behavioural, environmental and social cues (Duckworth & Sockman, 2012; Chang et al, 2013). Hormones act on multiple tissues and organs simultaneously and pluralistically alongside other hormones (Crespi, 2015). As a result, they have the potential to generate multiple, and potentially correlated, behavioural responses to a particular stimulus, providing a potential mechanistic link correlating behaviours over time and thus generating behavioural syndromes, i.e. personality (Réale et al, 2007; Wolf & Weissing, 2010).

Variation at a genetic level, particularly single nucleotide polymorphisms (SNPs), has been investigated in relation to variation in hormone expression and the affinities of hormone receptors in humans and other animals. For example, in humans, SNPs in the genes encoding the *TthII*I glucocorticoid receptor are associated with variation in circulating cortisol, the "stress hormone" (DeRijk, 2009), and in Mereno sheep (*Ovis aries*), allelic variation in the CYP17 gene correlates with variation in cortisol response to a pharmacologically-induced stress reaction (Qiu et al, 2016). Therefore, there is evidence that variation at a genetic level may be associated with variation in hormone expression or receptivity. A major recent interest within animal personality research is examining the association between variation in hormone expression and variation in personality expression (Fürtbauer et al, 2015).

Theoretically, endocrine functioning can have multi-modal effects on personality expression by determining the speed, strength and flexibility of behavioural responses to their immediate environment (Duckworth & Sockman, 2012; Hau et al, 2016; Taff & Visoutek, 2016). Endocrine studies of personality have most frequently focused on the hormonal stress response via monitoring of cortisol and other glucocorticoids (Koolhaas et al, 1999; Suomi et al, 2011; Fürtbauer et al, 2015). In vertebrates, the major response to a stressor is activation of the hypothalamic-pituitary-adrenal (HPA) axis which stimulates the redirection of energy and behaviour via glucocorticoids (Sapolsky et al, 2000). Animals, including humans, are subjected to stressors constantly, such as homeostatic stress in the form of body temperature and nutritional level variation, as well as less predictable and potentially severe stressors, such as the threat of predation or losing competitive encounters (Wingfield, 2005). In this respect, glucocorticoids are closely linked with an individual's response to its environment and thus much of its activity and behaviour. The hormonal stress response presents a valuable opportunity to examine an aspect of the state-dependent hypothesis previously described. If inter-individual variation in stress physiology exists, this may generate inter-individual variation in personality, and if hormonal stress responses to particular stimuli or environments are relatively constant for individuals, this may generate consistency in behaviour (Duckman & Sockworth, 2012). How HPA activity translates into personality is not consistent between species (Coppens et al, 2010). For example, in rhesus macaques, consistently aggressive individuals had high levels of circulating stress hormones (Higley et al, 1992), whereas in greylag geese (*Anser anser*) and three-spined sticklebacks (*Gastrosteus aculeatus*), shyer individuals had higher stress reactivity compared to their conspecifics (Kralj-Fišer et al, 2007; Fürtbauer et al, 2015).

Monitoring hormonal activity was for a long time limited to laboratory or captive populations of animals, or using invasive methodologies with wild populations. Whilst laboratory and captive studies provide valuable data for the study of behaviour, these animal populations may not entirely reflect the behaviour, social systems or physiology (and thus state) of wild conspecifics (Fusani et al, 2005). Similarly, trapping and invasive monitoring of wild and captive populations is often undesirable for ethical or practical reasons, it may affect the hormone levels detected and can lead to a sampling bias of only easily-trapped individuals (Biro & Dingemanse, 2009). This is particularly pertinent when trying to understand proximate associations to personality in natural, non-manipulated environments (Réale et al, 2007). Well-established methodology now allows hormone metabolites to be extracted from faecal or urine samples, and thus the non-invasive monitoring of hormone activity in individuals (Hodges and Heistermann, 2003). Therefore, researchers have the opportunity to examine the associations between glucocorticoids, and thus stress response, and personality in wild-living species. However, to date, few studies have addressed the endocrinology of personality with wild animal subjects, and where they have, invasive methodologies have been adopted (Cockrem, 2007; Montiglio et al, 2015). In the second results chapter of this thesis (chapter 4), the relationship between physiological stress response and personality expression in wild Barbary macaques is examined using non-invasive methods. These primates face a number of social and environmental stressors in their native habitat (Maréchal et al, 2011; McFarland & Majolo, 2013; Majolo et al, 2013; Young et al, 2014a). Few studies have attempted to link personality and stress response in a truly natural and heterogenic environment; therefore, this study makes a significant contribution to personality research by exploring an adaptive model of personality (state-dependence) in a cohort facing selective pressures relevant to the evolutionary history of the species.

1.5 Functional Outcomes of Personality

Functional studies of personality examine how different personality phenotypes interact with their environment and the potential fitness outcomes of these interactions (Dingemanse & Réale, 2005). For many animals, including humans, the social environment may be as important an influence on fitness as the climatic or non-social ecological environment (Silk, 2009; Formica et al, 2012; McFarland & Majolo, 2013; Lehmann et al, 2015). Living in social groups offers benefits such as increased detection and protection from predators, greater detection of food resources and access to mates (Krause & Ruxton, 2002). However, close-quarter associations with conspecifics also generate conflict for resources and increase potential exposure to pathogens (Krause & Ruxton, 2002). Evolutionary theory predicts that animals form and maintain groups when individuals can navigate their social environments in order to maximise the benefits and limit the costs of social living (Silk, 2014). In group-living animals, personality may contribute to optimising social outcomes for individuals.

Personality is predicted to be both shaped by and, in a complex feedback loop, to shape, social environments (Aplin et al, 2013; King et al, 2015; Sih et al, 2015). The “social niche” hypothesis states that personality arises and is maintained when group-living individuals segregate into particular social roles

(Bergmüller & Taborsky, 2010). For example, “bold” barnacle geese (*Branta leucopsis*) are more explorative foragers than “shy” geese, and drive the direction of foraging, resulting in segregation by personality during periods of resource acquisition (Kurvers et al, 2009; 2010). This in turn may have fitness consequences; bold and explorative individuals are predicted to encounter novel pathogens more frequently, either through exploration of novel resources such as food, or through interactions with non-group members or other species (Wolf & Weissing, 2010). This has been demonstrated in Siberian chipmunks (*Tamias sibiricus*); explorative individuals had significantly higher parasite burdens than their neophobic conspecifics (Boyer et al, 2010). Once pathogens have been encountered, personality could affect how effectively these are transferred throughout the group. Different personality phenotypes are expected to interact at different rates with different individuals (Krause et al, 2010). For example, in great tits and stickleback fish, bolder individuals have more social ties than shy individuals (Pike et al, 2008; Aplin et al, 2013). Certain highly social personalities may be “super spreaders” if they move more rapidly through their social environment and have social contact with a greater number of individuals, although linking personality to the social spread of disease is yet to be empirically explored (Kurvers et al, 2014).

Within the animal kingdom, there is high inter- and intra-species variation in how individuals congregate to form groups and the social structures that result from these congregations of individuals (Whitehead, 2008; Ilany & Akçay, 2016). In order to understand how personality shapes and is shaped by these social networks, researchers need to take a broader view of sociality beyond dyadic bonds (Krause et al, 2010). Social network analysis (SNA) is a valuable tool for relating inter-individual variation in phenotypes to sociality (Croft et al, 2008). Although the mathematics behind social networks has been explored since the 1930s, it is in recent decades that advances in computational power and novel software have seen a proliferation of interest and expansion of the techniques utilised in SNA (Farine & Whitehead, 2015). In social network theory, individuals are represented as ‘nodes’ and linked together by ‘edges’, which may be a measure of any biological relationship between individuals (Wasserman & Faust, 1994). Figure 1.1 illustrates an example of a social network and the characteristics that can be incorporated. Within personality research, SNA allows researchers to examine multiple factors such as: how personality influences the level of social integration for individuals (Pike et al, 2008; Croft et al, 2009; Aplin et al, 2013); how personality is related to “social phenotypes” by exploring whether individuals are socially consistent in terms of their network positions and how this is related to their behavioural consistency (Jacoby et al, 2014; Aplin et al, 2015); and whether personality affects assortment and segregation of individuals within social networks (Aplin et al, 2013). Each of these factors will influence the costs and benefits of group-living and thus analysing personality through the framework of SNA is a promising avenue for researchers. In the final results chapter of this thesis (chapter 5), SNA will be used to explore how personality is related social consistency, social integration and social assortment in wild Barbary macaques.

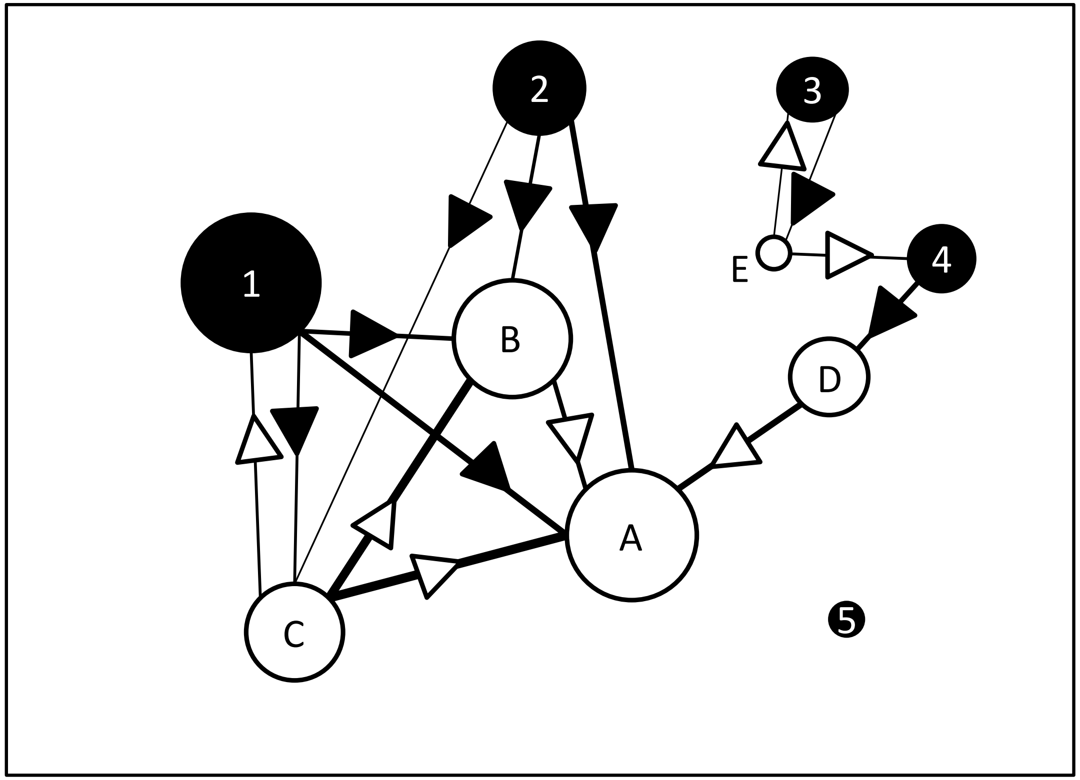


Figure 1.2: Example of a hypothetical social network where nodes symbolise individuals (females are white and labelled by letters; males are black and labelled by numbers) and are scaled according to rank (larger nodes indicate higher ranks). The edges/interactions between individuals are directed (indicated by arrow direction) and scaled by the strength of the association (thicker lines indicating stronger associations between the dyads). In this example, sex and rank characteristics appear to shape the network, with no intra-sex interactions among males, and interactions typically directed up hierarchies.

1.6 Present Project and Aims

Primate personality research has a long history, but in a limited number of species, predominantly in captivity, and without addressing adaptive models used to explain personality within the framework of evolutionary theory (Freeman & Gosling, 2010). Multi-method approaches to quantifying personality, i.e. incorporating all of the three approaches described, have the potential to avoid the shortcomings of singular approaches, although few studies have attempted this to date and hence the characterisations of personality we have for some species may be incomplete, particularly in terms of accurately exploring the mechanistic associations and functional outcomes of personality (Uher, 2008; Freeman et al, 2011; Iwanicki & Lehmann, 2015). This project used a multi-method approach to quantify personality in wild Barbary macaques, and then utilised non-invasive endocrinology and SNA to respectively examine the state-dependent and social-niche hypotheses for how personality is maintained in a wild, socially complex species.

Working with wild animals allows us to observe real-world selective pressures on personality, endocrine processes and sociality, such as predation or climatic factors (McDougall, 2006). Wild Barbary macaques live in groups of 15 to 88 individuals (Fooden, 2007; Majolo et al, 2013) and face a number of social, climatic, ecological and anthropogenic stressors (Maréchal et al, 2011; McFarland & Majolo, 2013; Majolo et al, 2013; Young et al, 2014a). They also form long-term inter- and intra-sex social bonds (Fooden, 2007; Young et al, 2014b), making them ideal subjects to explore in relation to sociality. Semi-free ranging and captive Barbary macaques have been found to be tolerant or egalitarian compared to the more despotic rhesus macaques (Thierry et al, 2000; Wendland et al, 2006). However, evidence to the contrary has been found in wild populations and more data from the wild has been called for to determine the naturally-occurring “social style” of Barbary macaques (Majolo et al, 2013).

To date, there are only two published studies pertaining to Barbary macaque personality, both of which employed the trait rating (questionnaire-based) methodology (Konečná et al, 2012; Adams et al, 2015). Konečná et al (2012) studied a group of semi-free-ranging macaques in Gibraltar (n = 27) and described a personality structure containing four components: “Friendliness”, “Activity/Excitability”, “Confidence” and “Opportunism”. Adams et al (2015) studied two wild groups of macaques in Morocco (n = 74) and also found a four-component structure to the personality of subjects: “Friendliness”, “Confidence” (both also found in Konečná et al, 2012), “Openness” and “Irritability”. Adams et al (2015) equated “Activity/Excitability” found in the previous study with the “Openness” found in their study, while “Opportunism” and “Irritability” were found to share a number of constituent traits. Nevertheless, despite using the same questionnaire, some differences in the personality structure of subjects were found between the studies and this requires further exploration.

It has been claimed that as the only African macaque species, Barbary macaques are the oldest species in the genus (Thierry et al, 2000). Therefore, there are advantages for future comparative studies and more generally within evolutionary personality research in developing a more complete assessment of Barbary macaque personality structure, such as has been achieved in chimpanzees (Freeman et al, 2013; Massen et al, 2013). Collectively across several studies, chimpanzee personality research has utilised all known personality assessment methodologies and identified a range of personality traits and dimensions (Freeman et al, 2013; Massen et al, 2013). The current project will be the first to attempt this in a non-hominid primate species and among the first studies within animal personality research to attempt concurrently assessing personality using all available methodologies with wild animal subjects.

This thesis specifically addresses the following research questions:

What is the structure of Barbary macaque personality and what are the advantages of the multi-method approach to personality quantification used in this study? (chapter 3)

Does inter-individual variation in stress physiology exist in Barbary macaques, and if so, is it related to inter-individual variation in personality? Is stress physiology stable within individuals and thus potentially a constraint on behavioural flexibility? (chapter 4)

What is the relationship between personality and sociality in wild Barbary macaques? Specifically, how does an individual's personality relate to an individual's social integration and does personality shape social network structure in this species? (chapter 5)

2| General Methods

2.1 Study Species

The *Macaca* genus, comprised of 20 extant species, is the most extensively studied group of monkeys (Thierry et al, 2000). Predominantly frugivorous, semi-terrestrial primates, macaques are also the most widely distributed non-human primate genus, with a composite geographic range that includes north western Africa, southern and eastern Asia (Fooden, 1982). The genus can be subdivided into three main species groups (Fooden, 1982): *silenus-sylvanus*, *sinica-arctoides* and the *fascicularis* group, although stumptailed macaques (*Macaca arctoides*) and Barbary macaques (*Macaca sylvanus*) have each been alternatively classified as their own species group (Morales & Melnick, 1998).

The Barbary macaque is probably one of the earliest phylogeographic offshoots of the genus and is now the most geographically isolated of extant macaque species (Fooden, 1982; Modolo et al, 2005). The species lives in multi-male, multi-female groups with typical sex ratios ranging between 0.6 and 1.6 females per male (Ménard, 2002). Sexual dimorphism is evident in Barbary macaques in relation to body weight and length, with adult males being longer (550-600mm) and heavier (15-17kg) than adult females (450mm, 10-11kg; Fooden, 2007). Wild Barbary macaques have an estimated lifespan of 15-17 years (Majolo et al, 2013) and reach sexual maturity at the ages of 6 in males and 5 in females (Ménard et al, 2013). They are highly seasonal breeders: the mating season occurs between October and January during which females show perineal swellings (Möhle et al, 2005). The mean gestation period is 163 ± 4.6 days with the birthing season typically in the months of April and May (Fooden, 2007). Males typically migrate at between 3-4 years old, although sexually mature males may permanently remain with their natal groups (Kuester & Paul, 1999).

Wild populations of the species are found in parts of Morocco and Algeria, with a geographic range from a latitude of around 36° 15′N to 36° 45′N and a longitude of around 7° 45′W to 5° 35′E (Fooden, 2007). A provisioned, semi-free ranging population exists on Gibraltar, which may have been introduced or is a remnant from the species' formerly European-wide distribution (Modolo et al, 2005). Within this geographic range, Barbary macaques colonize a variety of habitats, principally cedar-oak (*Cedrus atlantica* and *Quercus ilex*) and deciduous oak forests (*Q. faginea* and *Q. afares*), scrub, grassland and rocky ridges (Fooden, 2007). This species' geographic range places it in temperate cold climates, with populations found at elevations between 400 and 2,300m (Navaro-Cerillo, 2013). Consequently, wild Barbary macaques experience extreme seasonal climatic variations: summers are hot and dry with temperatures reaching 40°C, winters are cold and wet with temperatures below 0°C (Majolo et al, 2013). Temporal and geographic variation in habitat and climate necessitate ecological plasticity: Barbary macaques are generalist feeders (Ménard, 2002); however, varying habitat quality and diet composition have been shown to significantly influence the behavioural ecology and demographics of populations of the species (Ménard et al, 2013).

Group size is highly variable between populations: provisioned groups in Gibraltar are composed of around 60-80 individuals, in the Middle Atlas region of Morocco groups average 15-25 individuals (Majolo et al, 2013), whilst the largest known wild group size was 88 individuals (Fooden, 2007). In 2008, Barbary macaques were categorised as "Endangered" on the IUCN Red List

(IUCN, 2008). The worldwide population has decreased from 1974 estimates of approximately 21,000 to modern estimates of 6,000-8,000 (van Lavieren & Wich, 2010). Causes of this decline include habitat fragmentation, illegal capture of infants for the pet trade and habitat degradation from human encroachment in the form of pastoralism or tourism (Ménard et al, 2013). Habitat fragmentation has caused wild populations within the species to become isolated. Genetic analyses have revealed low genetic diversity within these sub-populations (von Segesser, 2002; Modolo et al, 2005), raising concerns about their viability and vulnerability to anthropogenic disturbance and infectious diseases (Majolo et al, 2013).

2.2 Study Site and Population

Data were collected at a study site in the oak and cedar forest near the city of Azrou, Morocco (33° 24′N, 05° 12′W; elevation 1,500-2,000m above sea level). This area is located within the Ifrane National Park, in the Middle Atlas Mountains. The climate at the site is highly variable throughout the year: between 1975 and 2004, the Ifrane Meteorological Station recorded maximum and minimum temperatures annually averaging 17.9 and 9.1°C in January and 30 and 15.6°C in August, respectively (Navarro-Cerrilo, 2013). For the same period, annual precipitation averaged between 700 and 1,200mm, whilst snow cover, on average, lasted for 15-30 days between November and March (Navarro-Cerrilo, 2013). Figure 2.1 illustrates average monthly temperatures (low and high) and rainfall in the region between the years 2000 and 2013 (www.worldweatheronline.com).

The forest surrounding Azrou is composed of various tree and bush species, principally *C. atlantica* sparsely mixed with a number of oak species

(*Quercus ilex*, *Q. faginea*, and *Q. canariensis*), Italian maple (*Acer opalus*), Oriental thorn (*Crataegus orientalis*), North African ash (*Fraxinus dimorpha*), common hawthorn (*Crataegus monogyna*) and red-berried mistletoe (*Viscum cruciatum*) (Navarro-Cerrilo, 2013). Other than the Barbary macaque, large mammal species that inhabit this forest include wild boar (*Sus scrofa*), jackals (*Canis aureus*), genets (*Genetta genetta*) and feral or locally-owned domestic dogs (*Canis lupus familiaris*) (Majolo et al, 2013). The forest is also extensively used by humans, containing several designated tourist sites, large patches reserved for pastoralism (grazing of goats, sheep and cattle) and numerous logging concessions (Ménard et al, 2013).

The forest region around Azrou is populated by approximately 1,000 Barbary macaques (van Lavieren & Wich, 2010). In January 2008, a longitudinal field project was established in the Middle Atlas Mountains by the University of Lincoln (UK), and the Ecole Nationale Forestiére d'Ingénieurs (Morocco) to study the ecology and behaviour of Barbary macaques (http://barbarymacaque.blogs.lincoln.ac.uk). This longitudinal study has five habituated groups of Barbary macaques (McFarland, 2011; Maréchal, 2015; Campbell, L.A.D, personal communication).

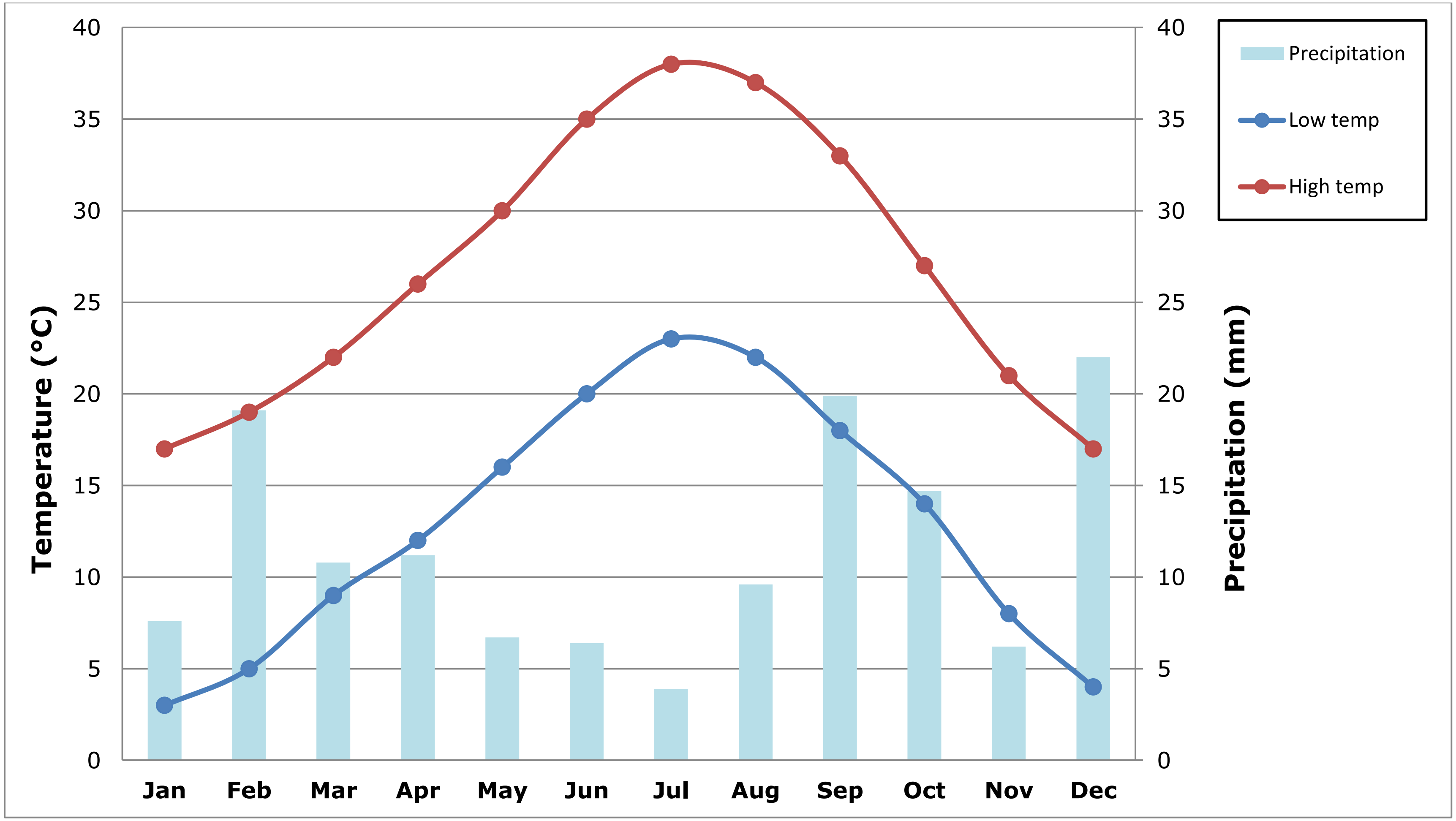


Figure 2.1: Average monthly temperatures (low and high) and precipitation in Azrou region between 2000 and 2013 (data source: http://www.worldweatheronline.com/azrou-weather-averages/ma.aspx).

2.3 Study Subjects

For the current study, two groups of fully habituated Barbary macaques were studied. The ‘Green group’ was first habituated in 2010 (McFarland, 2011) and has been studied continuously since this time. The ‘Blue group’ was first habituated in January 2013 (Waterman, personal communication, 2013). For this study, all the adults of both groups were the subjects. Both groups are fully habituated to human observers and could be followed at a 7m distance. The kinship between adults is not known in either group. In the Green group the mother/daughter relationships of the primiparous females is known.

Subjects were categorised by age/reproductive life stage: primiparous females (in first or second year of sexual maturation with anogenital swellings visible; Fooden, 2007), adult (sexually mature, no signs of physically aging; Fooden, 2007), and elderly adult (clear signs of aging, no anogenital swelling in females, loss of teeth and spinal osteoarthritis in both sexes; Bailey et al, 2014; Galbany et al, 2011a, 2011b). No individuals changed age category during the study period. Defintions of age classes can be found in table 2.1, along with counts per sex/age/class. Table 2.2 describes the sex, age and names of subjects of the current study.

During the course of this project (09/10/2013-06/03/2014 and 04/02/2015-18/04/2015), the groups had non-overlapping home ranges within Ifrane National Park, Morocco (figure 2.3). The Blue group’s home range is adjacent to the N13 road and consequently the group is frequently provisioned by tourists. The Green group is relatively isolated from human interaction and from tourism although it does experience anthropogenic disturbance from pastoral activity, such as the presence of farmers, herds of sheep and sheep-herding dogs.

Table 2.1: Age/sex classification of Barbary macaques (adapted from Fooden, 2007) and numbers of individuals per age/sex class for the Blue and Green group during the study period. The final number (recorded 18/04/2015) per age/sex class is given, with range given in brackets if numbers fluctuated during the study period.

Class	Age (years)	Definition	Blue	Green
Elderly adult male	~	Clear signs of aging, principally loss of teeth, hair and spinal osteoarthritis	1	2
Adult male	6+	Reach full body length and weight (550-600mm; 15-17kg); large ischial callosities; typically have notable main of hair around neck and shoulders in comparison to females	4 (4-6)	3
Subadult male	4-5	Testicles descend into scrota and become visible from a distance; canines lengthen to differentiate from female dentition	1 (1-3)	1 (0-1)
Elderly adult female	~	Clear signs of aging, principally lack of anogenital swellings, loss of teeth, hair and spinal osteoarthritis	2	0
Adult female	5+	Reach full body length and weight (c. 450mm; 10-11kg); anogential swellings clearly visible and often blue-grey in colour	5	7
Subadult and primiparous females	3-4	Cicumanal and lateral vulval swellings become apparent as slight pinkish bulges	1 (1-2)	3 (2-3)
Juvenile	1-3	Fully weaned and reduced association with mother	9 (9-11)	21 (19-21)
Infant	0-1	Born with black coats, changing to brownish pelage after 145 days; wean consistently up to 45 days, then intermittently until c. 1 year old	2 (2-4)	6 (3-6)
		Total numbers:	25 (25-34)	43 (36-43)

Table 2.2: Identities and class of study subjects.

Green Group	Class	Blue Group	Class
ANN	Adult ♀	CON	Elderly adult ♀
DAN	Adult ♀	ELI	Elderly adult ♀
HEL	Adult ♀	IZZ	Adult ♀
JOA	Adult ♀	NIC	Primiparous ♀
KER	Adult ♀	PEN	Adult ♀
REB	Adult ♀	SAR	Adult ♀
DAK*	Primiparous ♀	WAN	Adult ♀
KRI**	Primiparous ♀	GUL	Adult ♂
ART	Adult ♂	CAS	Adult ♂
GEO	Adult ♂	ISA	Adult ♂
MAC	Adult ♂	TIM	Elderly adult ♂
NOD	Elderly adult ♂	ROC	Adult ♂
OZZ	Elderly adult ♂		
SIM	Adult ♂		

* DAN is the mother of DAK, who was a sub-adult at the start of the study and became pregnant in first breeding season

** KER is the mother of KRI, who was a sub-adult at the start of the study and became pregnant in first breeding season

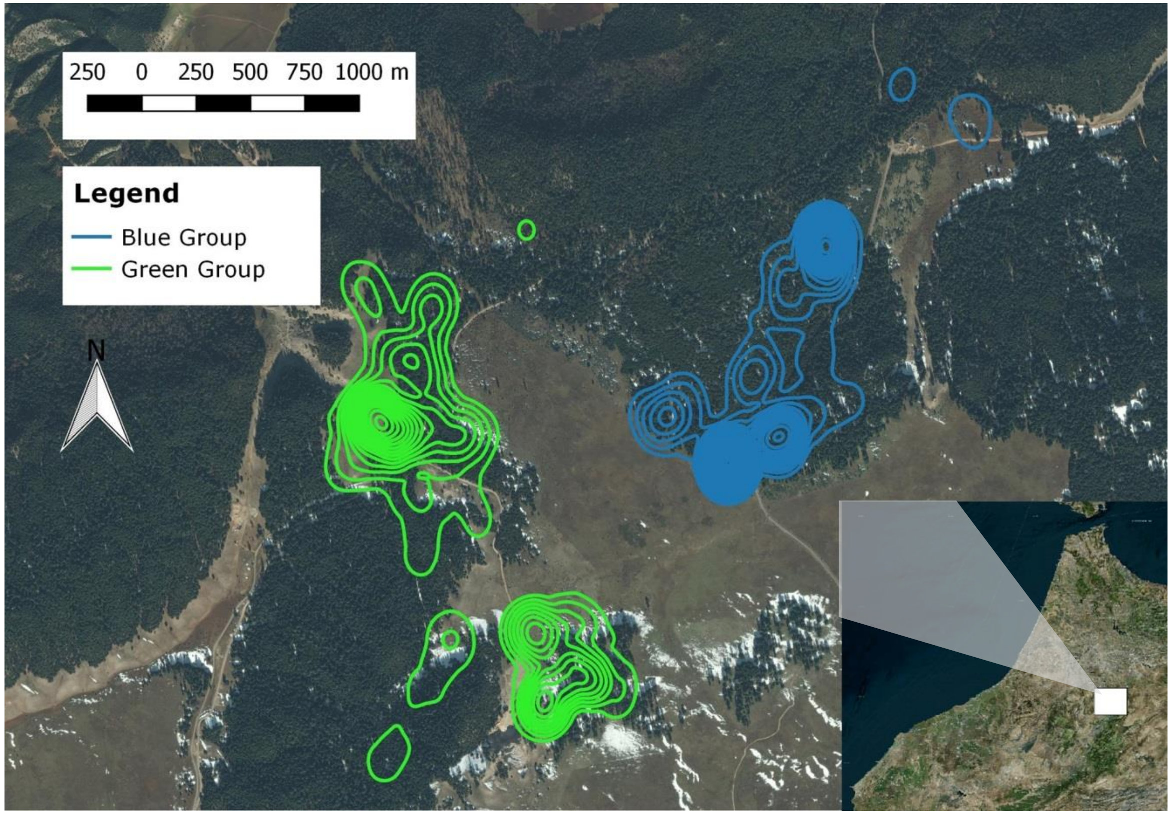


Figure 2.2: Home ranges of Blue and Green groups; located in the Middle Atlas mountain range of Northern Morocco (see inset). Home ranges are presented as fixed kernels: the contours represent the probability of a group occurring in that area, i.e. steeper contour represents greater probability of group being observed within that area; minimum probability 70.00% (Worton, 1989). Home ranges were calculated from hourly GPS recordings of group locations between October 2013-March 2014 and February-April 2015 (section 2.5; scan frequencies: n=9,759 for Blue group; n=9,671 for Green group).

2.4 Data Collection

Behavioural data collection and experiments were conducted from October 2013-March 2014 and February-April 2015, following a week-long pilot study conducted in May 2013. During the pilot, identities of the subjects were learned, familiarisation with the field site conducted, and preliminary data collection protocols and equipment tested. Questionnaire data were collected from participants intermittently throughout the entire study period (i.e. May 2013-April 2015). All data collection was conducted following ethical approval by University of Roehampton (appendix A1) and the receipt of research permits from Haut-Commissariat aux Eaux et Forêts et à la Lutte Contre la Désertification, Royaume du Maroc (appendix A2)

Research assistants (n=4) received training and only collected behavioural data following inter-observer reliability tests. For these tests, a focal observation of a subject was conducted simultaneously by all assistants and the principal investigator. Reliability in the durations and frequencies of behaviours observed by all researchers during these observations was then analysed using intraclass coefficients (ICC; Shrout & Fleiss, 1979). Only once an assistant recorded two consecutive tests with significant reliability ($p<0.05$) were they instructed to collect data to be used for the project.

2.4.1 Behavioural Sampling

Behavioural data were collected from near dawn (when it became light enough to see clearly and the subjects became active) to near dusk (when the sun began to set and the subjects climbed into sleeping sites in trees). The earliest the subjects were found was 06:30 and the latest time the subjects were recorded moving to sleep sites was 19:50; the mean duration for daily observational data collection was 8 hours (±2.5 hours; n=285 days). The Blue Group were followed for a total of 140 days, the Green group for 145 days. Behavioural data were collected through focal and scan sampling (Altmann, 1974) using a Psion handheld computer and The Observer XT software version 8.0 (Noldus Information Technology, 2008). Behavioural data have been used to calculate **dominance hierarchies** (section 2.4.4), **social networks** (section 2.4.7) and for **behavioural coding** methods for assaying personality (see section 2.4.5).

Focal sampling

Focal observational samples lasted 30 minutes. The order of subjects for focal samples was determined daily using a random order generator (http://www.random.org/lists). Subjects were not re-sampled until all other individuals had been sampled and never more than once on the same day. Table 2.3 shows the durations of focal samples per daily period per subject. A one-way ANOVA revealed subjects were sampled more frequently between 11:00-14:30, than for the other two time periods (F=41.85, df = 26, p<0.01).

During focal samples, activity state behaviours were recorded continuously. Contact, agonistic, solitary and sexual behaviours, as well as facial displays, vocalisations and anthropogenic interactions were all recorded as point events. Table 2.4 defines state behaviours and the categories of point events. A full ethogram with more detailed definitions of behaviours is provided in appendix A3. Samples where subjects were out-of-view for over 5 minutes were discarded. Across the whole study period, 1,308 hours of focal samples were collected, equating to 48.41(±1.64) hours per subject.

Table 2.3: Duration of focal samples (in hours) throughout the day for subjects.

Subject	07:00-11:00	11:00-14:30	14:30-1900
ANN	17.26	18.19	13.05
ART	15.89	19.12	14.86
CAS	18.68	16.00	15.63
CON	13.42	18.94	11.83
DAK	15.06	19.19	13.95
DAN	12.35	19.67	18.56
ELI	12.82	26.75	10.81
GEO	18.48	19.52	13.38
GUL	14.94	19.11	17.64
HEL	11.32	25.20	12.36
ISA	10.35	22.72	17.56
IZZ	16.53	16.62	17.20
JOA	16.50	17.95	16.95
KER	15.46	16.55	18.45
KRI	15.47	20.13	12.85
LEW	13.38	21.55	12.90
MAC	11.94	24.73	14.75
NIC	15.43	18.09	14.51
NOD	15.47	15.53	19.13
OZZ	12.91	20.33	15.92
PEN	15.44	23.66	12.87
REB	11.77	20.76	16.15
ROC	11.92	21.13	15.41
SAR	14.43	18.33	18.14
SIM	15.46	21.09	11.26
TIM	13.92	21.24	12.43
WAN	17.49	21.12	11.26
MEAN	14.60	20.12	14.81
(±SD)	(±2.21)	(±2.78)	(±2.53)
TOTAL	394.07	543.22	399.82

Table 2.4: Ethogram of general activity behaviours and categories for point events. Partners and/or nearest neighbours were recorded where appropriate. Behaviour definitions adapted from McFarland (2011).

State Behaviour	Definition
Travel	Subject is moving and does not appear to be moving to food source or other monkeys. This includes short bouts of sitting and looking for the next steps to take or at the next individual in line.
Rest	Subject is stationary and not doing any other behaviour (not feeding, travelling or social, i.e. not being groomed)
Feed	Subject is ingesting food; putting food into mouth AND Also chewing food in a feeding bout
Co-feeding	As above, but the subject is within 5m of another monkey which is also feeding
Foraging	Subject is breaking stems, stripping leaves from twigs, turning over rocks for insects but not feeding. Includes short periods of locomotion like walking to the next shrub
Give groom	Monkey grooms hair of the other, it watches the groomed place on the other‘s body, using its fingers or mouth, it may or not pick up some particles
Receive groom	Monkey(s) grooms hair of the subject, it watches the groomed place on the subject‘s body, using its fingers or mouth, it may or not pick up some particles
Groom simultaneous	Subject is both grooming another monkey and being groomed by another monkey
Self-groom	Subject grooms its own hair, it watches the groomed place, using its fingers or mouth, it may or not pick up some particles
Playing	Subject is play-fighting or chasing another monkey, no aggression is evident in the activity
Vigilance	Subject checks the area around itself, may be scanning conspecifics or potential threats outside of the group
Out-of-sight	Subject moves out of observer’s vision

Point Events	Behaviours
Contact/proximity behaviours	Approach, departure, supplant, embrace, genital touch, present for grooming, mock bite, kiss, submission, sandwich and touching
Agonistic interactions	Charge, chase, lunge, slap, push and pull, jump on, check look, mount, ground lap, aggression and defence support
Sexual behaviours	Present sex, reject sex, refuse sex, sex dance, reach back, start copulation, finished copulation and unfinished copulation
Solitary behaviour	Tree shake, masturbate, self-scratch, body-shake, gaze and yawn
Facial displays	Stare, open mouth, bare teeth, eyebrow lift
Vocalisations	Lipsmack, teeth chatter, fear scream, aggression scream, long call, grunt, copulation call, pant
Anthropogenic interactions	Berber threat, Berber attack, tourist threat, tourist attack, Berber provision, tourist provision, begging

Scan and *ad libitum* sampling

At the start and end of each focal sample, the proximity of group members around the focal subject was recorded. The identities of individuals were recorded at three distances: 0-1m (within reaching distance); 1-5m (typical nearest neighbour distance range for terrestrial primates [White & Chapman, 1994]); and 5-10m (distance at which individuals may be considered available bystanders for social interactions; Young et al 2014b).

Hourly scan samples of all subjects were conducted, recording group spread, subject activity (see table 2.5 for definitions) and the spatial position of subjects within the group (either central or peripheral). The direction and centre of the group was determined from group spread and activity recordings at the start of the scan, facilitating the subsequent categorisation of individual spatial positions. These data were used as variables for assessing personality (section 2.6).

In addition to scan and focal data, some behavioural data were collected using *ad libitum sampling*. All occurrences of supplants and aggression not involving the focal subject were recorded. Supplant and aggression data from focal and *ad libitum* data were included in dominance hierarchy calculations (section 2.4.2). In addition, all occurrences of copulations were recorded and used to determine mating season (section 2.4.4).

Table 2.5: Definitions for hourly behavioural scan samples. In the case of subject general activity, nearest neighbour, distance to nearest neighbour (0-1m, 1-5m and 5-10m) and direction of activity (for grooming only) were also recorded.

Scan sample	Category	Definition
Group spread	Clumped	Maximum distance between peripheral individuals (front and back; both sides) is less than 30m
	Moderate	Maximum distance between peripheral individuals (front and back; both sides) is less than 75m
	Dispersed	Maximum distance between peripheral individuals (front and back; both sides) is greater than 75m
Subject general activity	Travel	Majority of the group/subject is travelling and not obviously foraging as they travel
	Rest	Majority of the group/subject is stationary and not engaging in social behaviours or feeding/foraging
	Feeding/foraging	Majority of the group/subject is searching for, handling or consuming food items
	Social	Majority of the group/subject is playing, mating or grooming (for subject general activity, "Grooming" is a distinct activity)
	Vigilance	Majority of the group/subject is surveying general area
	Anthropogenic	Majority of the group/subject is involved in an anthropogenic interaction, e.g. begging or being threatened by shepherds
	Grooming (subject only)	Subject is either grooming the hair of another monkey or another monkey is grooming its hair

2.4.2 Female Reproductive State

Female reproductive state was determined from daily visual assessments of anogenital swellings using a graded methodology adopted from Young et al (2013). Table 2.6 outlines the classification of swelling sizes. Swelling data were used to calculate mating and non-mating season (section 2.4.3).

Table 2.6: Classification and description of different female anogenital swelling sizes; adapted from Young et al, 2013.

Grade	Description
0	Swelling is completely absent; maximal degree of skin wrinkling
1	Partial sign of swelling, wrinkling of skin still visible
2	Swelling clearly visible, genital structures protrude clearly from body
3	Swellings are completely turgid with no sign of wrinkles

2.4.3 Field Data Collection Time Periods

Field data (behavioural and faecal samples) were collected during two field trips: the first between 09/10/13-16/03/14; the second between 04/02/15-18/04/15. Data were divided into three time blocks based on mating season and chronological order; this was done to analyse consistency in a number of variables over time and contexts (table 2.7). The original intention was to collect data across four time blocks and including two full mating seasons; however, there were issues pertaining to field permits at the start of the second field season. Mating season was defined as the time period between the first and last observed "complete" copulation (i.e. the male was observed to have ejaculated; Young et al, 2013) in the group. In the Blue group, one male (CAS) and one female (ELI) were observed copulating continuously throughout all time blocks. However, ELI appeared to no longer be cycling (based on lack of variation in anogenital swelling) and had not given birth to an infant in the previous three years. Therefore, these copulations were considered anomalous and excluded when defining mating season.

Table 2.7: Time periods for field data collection.

Time block: Season	Dates	Duration (days)	Observation time per subject (hrs)
Blue Group			
1: Mating	11/10/13- 20/01/2014	101	15.86 (±1.90)
2: Non-mating 1	21/01/2014- 05/03/2014	43	14.04 (±0.87)
3: Non-mating 2	04/02/2015- 18/04/2015	73	17.38 (±0.23)
Green Group			
1: Mating	09/10/13- 10/01/2014	93	16.87 (±1.11)
2: Non-mating 1	11/01/2014- 06/03/2014	54	13.37 (±0.48)
3: Non-mating 2	04/02/2015- 18/04/2015	73	17.50 (±0.38)

2.5 Dominance Hierarchy Calculations

Data from focal samples and *ad libitum* scan samples were used to calculate dominance hierarchies. Dyadic interactions of aggression (contact and non-contact) and submission were used for rank calculations. These calculations were performed using an Elo-rating procedure, which calculates ranks based on the sequence in which dyadic interactions occur (Neumann et al, 2011). At the start of a sequence, all individuals are assigned the same predefined rating

(1000). Following an interaction, the winner gains points while the loser loses points; the number of points lost/gained is determined by the probability that the higher-rated individual wins (Elo, 1978). Depending on who wins, ratings are updated accordingly (Neumann et al, 2011):

Higher-rated individual wins: $\text{WinnerRating}_{new} = \text{WinnerRating}_{old} + (1 - p) \times k$

$\text{LoserRating}_{new} = \text{LoserRating}_{old} - (1 - p) \times k$

Lower-rated individual wins: $\text{WinnerRating}_{new} = \text{WinnerRating}_{old} + p \times k$

$\text{LoserRating}_{new} = \text{LoserRating}_{old} - p \times k$

where, p = probability of high-rated individual winning (function of absolute differences in ratings between the two individuals)

k = constant determining rating points gained or loss (here, 100)

The Elo-rating procedure thus provides an iterative and dynamic rank calculation, meaning ranks for individuals can be determined at specific dates. The stability of the hierarchy at any date can be determined from the index, *S*. *S* is the ratio of rank changes per individuals present over a given time period and can range between 0 to 1, where 0 indicates a completely unstable hierarchy, in which the ordering reverses every interaction, and 1, in which the ordering is completely stable and no rank changes occur (Neumann et al, 2011).

2.6 Personality Assessment

Three main approaches currently exist to characterise and quantify animal personalities; all three were used in this study: (i) behavioural coding in which animals are observed in a non-manipulated environment and the frequencies of behaviours associated with personality are recorded (Vazire et al, 2007); (ii) subjective observer ratings in which human observers are presented with questionnaires which score observed individuals on the relative presence or absence of particular personality traits (Stevenson-Hinde and Hinde, 2011); and (iii) experimental protocols which seek to elicit personality-associated behaviours from subjects and record the frequency of their expression (Fairbanks & Jorgunsen, 2011). Full details of the methodologies used to quantify personality are provided in chapter 3; brief summaries of the approaches used are provided here. Details on the statistical approaches used in these quantifications are introduced in this section and elaborated in chapter 3.

For **behavioural coding**, behaviour variables were extracted from both focal and scan sample observation data. Thirty-one behaviours were chosen based on relevance to Barbary macaque socioecology (Hodge & Cortes, 2006; Koski, 2011; Neumann et al, 2013; definitions are provided in table 2.8). Grooming diversity index (GDI) was calculated using the Shannon-Weiner diversity index (Cheney, 1992):

$$\mathrm{GDI} = H/H_{max}$$

$$H = -\mathrm{SUM}(p_i x \ln[p_i])$$

$$H_{max} = \ln(N-1)$$

where p_i is the proportion of individuals grooming effort given to the $_i$th individual and N is the number of individuals in the group

Repeatability analysis determined if subjects were consistent in the frequencies, durations and proportions of these behaviours across the three time blocks (section 2.9.1; Nakagawa & Schielzeth, 2010). Factorial analyses were then applied to consistent behaviours to identify suites of correlated variables, i.e. personality constructs (Budaev, 2010; Koski, 2011).

For **subjective trait assessments**, researchers (n=8) completed a questionnaire for each subject consisting of 51 items (personality traits; see appendix A4 for copy of questionnaire). A score of "1" suggests the trait is absent in the subject, whereas a score of "7" implies the subject has exhibited "extreme amounts" of the trait. Inter-rater reliability for item ratings was calculated using intraclass correlation coefficients (ICC; Shrout and Fleiss, 1979). For significantly reliable items ($p<0.05$), mean rating values were calculated for each subject. Principal components analyses were conducted on these mean values to determine personality components; ICC were then used to determine temporal consistency of components across seasons (n=3).

Experimental assays were used to quantify the degree to which subjects expressed two personality traits: boldness, defined as responses to risky but non-novel stimuli, and exploration, defined as responses to a novel but non-risky stimuli (Réale et al, 2007). For the boldness assay, playback experiments were conducted: subjects were presented with audio samples of non-group conspecifics intended to simulate an inter-group encounter. Following the presentation of the stimulus, a focal observation was performed on a subject using the same ethogram described in section 2.4.1. In addition, several assay-specific behaviours were recorded (see table 2.9). Repeatability analysis determined if subjects were consistent in the frequencies, durations and proportions of these behaviours across experimental treatments (section 2.9.1; Nakagawa & Schielzeth, 2010). Principal components analyses were then applied to consistent behaviours to identify suites of correlated variables and thus indices of response to the stimuli (Carter et al, 2012). For the exploration assay, novel object experiments were conducted: subjects were presented with treatments (brightly coloured toys or household items that had not been observed occurring in the forest) and one control (bundles of fallen branches or stones; see appendix A5 for photographs of all treatments and an example of a control object). Experiments began when the first group member (including infants and juveniles) entered within 20m of the object. Once experiments commenced, a 30 minute focal observation of the object was conducted; the observer recorded each individual (including infants and juveniles) which entered or left proximity (20m) of the object. During all instances of interactions with the object (see table 2.9), the behaviours and the distance of the subjects from the object were recorded. As with the boldness experiments, an index of exploration was derived from repeatability analyses and PCA (Carter et al, 2012).

Table 2.8: Variables used for behavioural coding.

Variable	Definition
Activity	Proportion of focal observation not spent resting or self-grooming
Submissions	Frequency of submissions per focal observation
Retreats	Frequency of retreats per focal observation
Supplant	Frequency of supplants per focal observation
Self-grooming	Proportion of focal observation spent self-grooming
Self-scratch	Frequency of self-scratches per focal observation
Body shake	Frequency of body shakes per focal observation
Yawn	Frequency of yawns per focal observation
Tree shake	Frequency of tree shakes per focal observation
Dominance mounts	Frequency of dominance mounts given per focal observation
Groom	Proportion of focal observation spent grooming with other monkeys
Grooming density	Total number of individuals subject grooms in scan and focal samples divided by all available grooming partners (juveniles and infants considered collectively)
Grooming diversity	Measure of diversity of grooming given (Shannon-Weiner diversity index; see text for formula)
Vigilant	Proportion of focal observation spent vigilant
Contact aggression	Frequency of contact aggressions given per focal observation
Non-contact aggression	Frequency of non-contact aggressions (lunge, charge, chase, ground slap) given per focal observation
Facial displays	Frequency of facial displays (open mouth, bared teeth, stare, teeth chatter, lipsmack; each display considered as an individual variable) given per focal observation
Embrace	Frequency of embraces given per focal observation
Genital touch	Frequency of genital touches received per focal observation
Sandwich	Frequency of sandwiches per focal observation
Edge of group	Proportion of scans observed on the edge of the group
Centre of group	Proportion of scans observed in the centre of the group
Neighbours 0-1m	Average number of individuals at 0-1m in scan samples
Neighbours 1-5m	Average number of individuals at 1-5m in scan samples
Neighbour 5-10m	Average number of individuals at 5-10m in scan samples
Approach	Frequency of 5m approaches given without negative responses (i.e. aggression) per focal observation

Table 2.9: Behaviour variables used for personality assessments utilising observational data.

Behaviour	Definition
Playback/Object Experiments	
Attention stimulus	Subject orientates its head towards the stimulus and sustains a gaze at the stimulus for at least two seconds
Approach stimulus	Subject moves purposefully in the direction of the stimulus over a distance of 1m or more. The subject maintains attention to stimulus as it approaches
Flee stimulus	Subject darts directly away from stimulus over 1m or more
Threaten stimulus	Subject bares teeth or screams in the direction of the stimulus
Object Experiments Only	
Touch stimulus	Subject briefly touches the stimulus in a probing manner
Hold stimulus	Subject holds, handles or manipulates stimulus with hands or mouth

2.7 Stress Physiology Data

Stress response in mammals is generally mediated by the hypothalamic-pituitary-adrenal axis (HPA), a complex set of feedback interactions between the hypothalamus, pituitary and adrenal glands (Herman & Cullinan, 1997). Activation of the HPA axis ultimately results in the production of glucocorticoids, such as cortisol. Metabolised glucocorticoids are eventually excreted in either urine or faeces, presenting the opportunity to monitor the stress state of an animal non-invasively (Hodges & Heistermann, 2003). In this project, faecal samples were collected and analysed in order to quantify faecal glucocorticoid (fGC) concentrations of subjects as a measure of stress and relate this to personality expression.

2.7.1 Faecal Sample Collection

Faecal samples were collected opportunistically throughout the study period. Attempts were made to collect one sample per subject every five-six days. Cortisol secretion follows a diurnal pattern in mammals (Hodges and Heistermann, 2003). To control for this, sampling effort was concentrated between the hours of 07:00-12:00; however, if no sample had been collected for an individual towards the end of a weekly collection cycle, any opportunistic sample would be collected. Samples were collected within 15 minutes of defecation: the faeces were first homogenised and a 3-5g sample portioned into a 30ml Azlon tube (Azlon 7BWH0030 N, Azlon, Stone, Staffordshire, UK), which in turn was placed in an ice bag and kept cold before being transferred to a freezer (-20°C) at the end of the day. Faeces that were contaminated with urine or appeared diarrhoeal were not sampled. In total, 876 samples were collected during the study and transported back to the University of Roehampton (following receipt of an attestation of health for the subjects from Moroccan authorities [appendix A6] and using a DEFRA import licences [appendix A7]).

2.7.2 fGC Extraction

Glucocorticoids were extracted from the faecal samples at University of Roehampton. Samples were freeze dried (Edwards Freeze Dryer Modulyo EF4), pulverised using a pestle and mortar, any undigested material (seeds, nuts etc) removed, and the remaining dry faecal matter weighed. Single extraction (Ziegler et al, 2005) was used: steroid hormones were extracted from 50-90mg of dried faecal matter with 2mL of 80% methanol. Samples were placed in a centrifuge at 4500rpm and 4°C for 20 minutes. Supernatants were removed and stored at -20°C. Recovery of a radio-labelled steroid found 85.03% of radio-labelled estradiol was recovered from 12 control samples using this steroid extraction method with samples from the same species and site (Kaburu, 2009).

2.7.3 Enzyme Immunoassay

Hormone analysis was performed using an enzyme immuno-assay (EIA; Engvall 1975; Crowther, 1998; Lequin, 2005). Concentrations of fGC were measured using a competitive binding assay, 5 β -androstane-3α, 11 β -diol-17-one, which has previously been validated for the measurement of glucocorticoid metabolites in Barbary macaques (Heistermann et al, 2006). Assays are subject to issues with cross-reactivity, (Hodges and Heistermann, 2003), whereby antigens besides those of interest may bind to the target antibody. Cross-reactions to the 5 β -androstane-3α, 11 β -diol-17-one assay are 3.4% for 5b-androstane-3a-ol-17-one, 1.8% for 11-oxo-etiocholanolone and <0.1% for corticosterone, testosterone, 5a-androstane-3, 17-dione, 5b-androstane-17-one, dehydroepiandro-sterone and androsterone (Ganswindt et al, 2003).

Faecal extracts and standard solutions were diluted in assay buffer (0.04M phosphate-buffered saline, pH 7.2). A reference standard curve was created from 8 serial dilutions of a known concentration (12,500pg/50µl) of the assay, generating 9 concentrations in the range of 2.43-624pg/50µl. To determine the dilution factor for samples, six samples of presumed low, medium and high GC concentrations (based on time in season for males or reproductive state for females, e.g. high concentrations for males in November [peak breeding season] and females in March [during pregnancy]) were diluted in ranges of 1:10-1:160.

These dilutions were examined for parallelism relative to the standard curve (see figure 2.4). Analysis of the parallelism of dilutions determined that samples should be assayed at a dilution of 1:40, as this would yield concentrations within the linear range of the standard curve.

For this study, 96-well micro-titre plates were pre-coated with anti-rabbit immunoglobulin, which was developed in sheep. Appendix A8 illustrates the layout of the plates and describes the plating procedure. Ascent software (Thermo Labsystems, 2002) calculated EIA concentrations; fGC concentrations could then be calculated from EIA concentrations by standardising for dry faecal weight, dilution and extraction efficiency:

$$fGC = \frac{\text{EIA concentration (pg)}x\ Exctract\ volume\ (3000\ \mu\text{l})x\ Dilution\ factor\ (40)x\ (100\ /factor\ 85.1)}{Dry\ faecal\ weight\ (g)x\ Sample\ volume\ (50\mu\text{l})x\ 1000\ *}$$

** conversion factor (pg to ng; 1000)*

Mean intra-assay coefficients of variation (calculated from quality control wells on plates) were 3.68% for high and and 6.51% for low (n= 33 plates). Inter-assay coefficients of variation were 7.00% for high and 11.67% for low (n = 66 quality controls). The 90% binding glucocorticoid concentration (measures of assay sensitivity for use in comparisons between different studies) was 1.83pg/50µl.

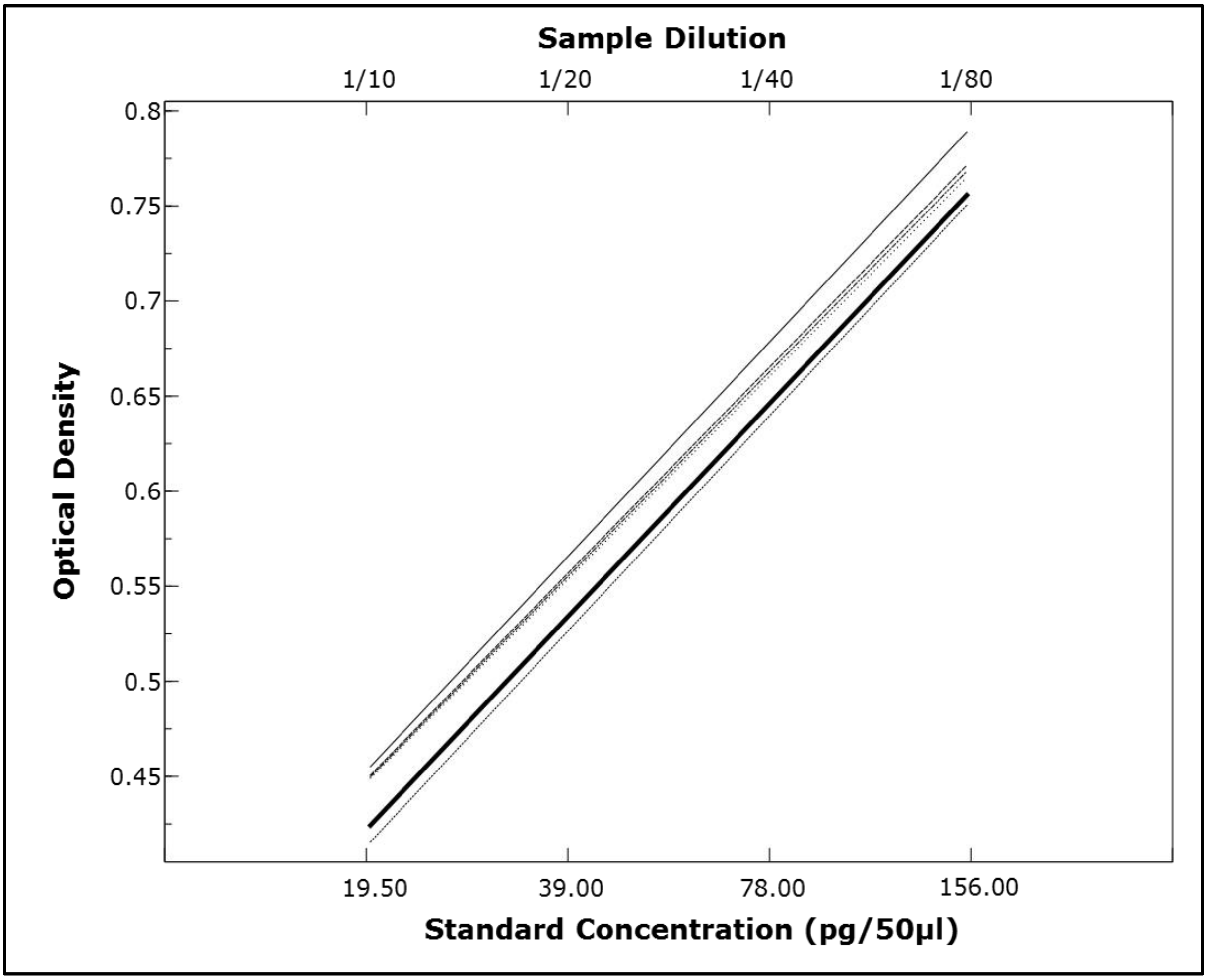


Figure 2.3: Parallelism test plotting regression lines of optical density values against dilutions (for selected samples; dashed or grey lines) and against standard curve concentrations (solid black line).

2.8 Social Network Analysis

In order to examine the relationship between personality expression and sociality in Barbary macaques, social network analysis (SNA; Wasserman and Faust, 1994) was performed using R version 3.0.3 (http://www.r-project.org). Full details on SNA are provided in chapter 5 but introduced briefly here.

Behavioural data were divided into three time blocks based on mating season and chronological order (table 2.7). For each of the two groups and for each of three time periods, four social networks were constructed: aggression, grooming, nearest neighbour and co-feeding. Constructed networks were then used to calculate individual measures of social integration for subjects (see table 2.11; adapted from Wey et al, 2008; Croft et al, 2008; Farine & Whitehead, 2015). Justifications for the use of these measures, and not others, are explored in more detail in chapter 5. Strength and betweenness were calculated using the *tnet* package (Opsahl, 2009), eigenvector centrality and individual clustering coefficient were calculated using the *igraph* package (Czardi & Nepusz, 2006). Phenotypic assortment (personality, rank, age and sex) in social networks was analysed using multiple regression quadratic assignment procedure (MRQAP) analysis and the *asnipe* package (Farine, 2013).

Table 2.10: Definitions and calculations for SNA measures (Croft et al, 2008; Wey et al, 2008; Farine & Whitehead, 2015).

SNA measures	Definition	Calculation
Strength (in and out)	Sum of all edge weights connected to the node	N/A
Betweenness centrality	Centrality based on number of shortest paths between every pair of other group members on which the focal individual lies	$B_i = \sum_{j=1}^{N} a_{ij} w_{ij}$ Where, a_{ij} is the adjacency matrix between nodes *i* and *j* of paths and w_{ij} the weighted matrix between nodes *i* and *j*
Eigenvctor centrality	Centrality based on the shortest path length between a focal individual and all other members of the social group	$x_i = 1/\lambda \sum_{j=1}^{n} A_{ij} x_j$ Where, xi = the score of th i-th individual, Aij = the adjacency matrix of the network and where λ is a constant
Individual Clustering Coefficient	Proportion of a given individual's social partners who are partners with each other	$c_i^w = \frac{1}{s_i(k_i - 1)} \sum_{j,h} \frac{w_{ij} + w_{ih}}{2} a_{ih}, a_{ij}, a_{jh}$ Where, $\frac{1}{s_i(k_i-1)}$ is a normalisation factor to account for the weight of each edge times the maximum possible of neighbourhoods of three nodes (triples) it may participate with; the remainder of the equation sums edge weights in these triples, e.g. *i*, *j* and *h*)

2.9 Statistics

2.9.1 Repeatability Analysis

Personality is defined as intra-individual consistency and inter-individual variation of behaviour (Réale et al, 2007). To measure intra-individual consistency in behaviour, and other factors which may be proximate to, or a consequence of, personality, consistency of these variables was tested using an ANOVA-based measure of repeatability, R_A. This method treats individual subjects as factorial predictors of repeatability (Nakagawa & Schielzeth, 2010) and determines significance based on a randomisation procedure: variables were randomised between factors (subjects) without replacement 1000 times and R_A calculated for each randomisation of the data; the p-value is calculated as the proportion of simulations that results in a random R_A greater than or equal to the observed R_A. R_A and p-values were calculated using the *rptr* package in R (Nakagawa & Schielzeth, 2010).

2.9.2 Modelling Approaches

A variety of linear and linear-mixed effect (LMEs) models was used to explore relationships between variables throughout the study. For each model, dependent variables were tested for normality using Q-Q plot visualisations and the Shapiro Wilks test (Zuur et al, 2011). If the distribution of variables was non-normal, $\log_{10}$ transformations were used. Collinearity of fixed factors was examined using variance inflation factors (VIF) and the *car* R package (Fox & Weisberg, 2011). If the VIF of a categorical fixed factor exceeded 2.5 (Field et al, 2012), each category was analysed in separate model. Collinearity was not observed between continuous variables.

Model selection was performed in chapter 4, where the relationships between the expression of personality, stress physiology and life history measures were explored, as it was not possible to make *a priori* predictions about which personality constructs would necessarily be related to these factors. For model selection, Akaike's information criterion (AIC) and maximum likelihood optimisation were used to simplify the best fit model (Burnham & Anderson, 2004). AIC model selection uses information theory whereby models are selected based on a trade-off between best fit and the complexity of the model, with a lower AIC value indicating a model with a better fit to the data (Akaike, 1974; Raferty, 1995). During the model selection process and the removal of fixed factors, the change in AIC (ΔAIC) between models was calculated. Models with AIC values differing from the best fit model by two or less were selected as substantially supported and results from these models considered (Raferty, 1995; Burnham & Anderson, 2004).

Best fit models were compared to a null model, i.e. an intercept-only model, using likelihood ratio tests and considered significantly different when $p<0.05$ (Bolker et al, 2009). To examine the relationship between the dependent variable and the remaining fixed factors within the best fit models, Wald logistic regression tests were performed, with factors considered significant when $p<0.05$ (Bolker et al, 2009). To illustrate the relationship between dependent variables and fixed factors, scatterplots are presented using the predicted values for the dependent variables from models, plotted against the fixed factors. For each plot of the predicted values, error bars are included representing the residual values (i.e. the difference between the predicted values and the observed values) to illustrate how well the model described observed data. Where an interaction between a categorical and continuous variable was found to have a significant relationship with the dependent variable, scatterplots for each category are presented alongside each other to illustrate variation between the categories.

Model selection approaches are contentious (Johnson & Omland, 2004) but elements of this project are exploratory and model selection was required to provide a simplified model (eschewing over-fitting and favouring the principle of parsimony), which was tested for significant differences from a null model, with assessments of the fit of the model made *prior* to any null hypothesis testing of the individual relationships within the best fit model (Burnham & Anderson, 2004; Bolker et al, 2009).

All models were visually inspected using Q-Q and Cook's Distance plots, where residuals are plotted against theoretical quartiles and leverage respectively to visually inspect the fit of the model (Field et al, 2012). If outliers or data points with high leverage were identified, these were removed to improve the fit of the model.

All models were fitted in R 3.0.3 using the *nlme* (Pinheiro et al, 2016) and *MASS* (Venables & Ripley, 2002) packages. Tests for normality and Q-Q plots were performed using IBM SPSS Statistics 21 (IBM Corp, Armonk, NY).

3| Quantifying Personality in Barbary Macaques: A Multi-Method Approach

Abstract

Animal subjects within personality research offer the opportunity to objectively explore the behavioral ecology of personality, as well as examine the evolutionary history of personality traits via phylogenetic comparisons. Three main approaches exist to quantifying personality in animals: Behavioral coding is functionally valid (reflects naturally occurring behavior) but may not include rare behaviors, which can be elicited in experimental assays. Subjective trait assessments use a standardised method, allowing for easy comparisons between studies, but, as with experimental assays, the personality constructs may not be functionally valid and the method is inherently subjective. Previous research on Barbary macaque (*Macaca sylvanus*) personality using subjective trait assessments found inconsistencies in personality structure between studies. Therefore, in this study, a multi-method approach incorporating all described methodologies was used to quantify personality in Barbary macaques in an effort to improve our understanding of personality in this species, as well as to explore the benefit of using all three methods simultaneously. The multi-method approach generated a more detailed characterisation of personality than previous studies in Barbary macaques and allowed for testing the functional, convergent and discriminant validity of quantified constructs. Seven personality constructs were quantified: Excitability, Sociability, Tactility, Confidence, Introversion, Boldness and Exploration. Results from this study demonstrate that a multi-method approach is plausible, even in wild primate subjects, and is

beneficial for achieving a characterisation of personality that is detailed, valid and cross-species comparable.

3.1 Introduction

Historically, evolutionary biologists have assumed that selection should predominantly favour being behaviourally flexible (West-Eberhard, 1989; Wilson et al, 1994) or that variation between individuals in behavioural strategies represents "noise" and deviation from the mean of a single, optimal, adaptive strategy (Weiss & Adams, 2013). However, studies in humans and a broad range of non-human animals (hereafter animals) demonstrate that individuals are predisposed to react to their environment in a predictable and consistent manner and that these reactions vary consistently between individuals (Sih et al 2004; Réale et al, 2007; Freeman et al, 2011). Understanding the mechanisms and consequences of this intra-individual consistency and inter-individual variation in behaviour, i.e. personality, has become a major focus of research within psychology, behavioural and evolutionary ecology (Réale et al, 2007; Carter et al, 2013).

Human personality research is often hampered by our species' longevity and difficulty collecting objective observational data (Gosling, 2001). Compared to human personality studies, animal models potentially offer more detailed and objective behavioural observations in real-world scenarios, the opportunity to closely monitor personality-associated physiological processes, and shorter-timeframe longitudinal studies (Mehta & Gosling, 2008). However, the advantages of animal models are offset by concerns pertaining to how personality can be measured reliably in animals and the degree of objectivity of personality data collected (Vazire et al, 2007). For comparative personality research to be effective, studies must establish "functional equivalence" for the personality traits being examined, i.e. traits defined and quantified in one species must be comparable to those using similar terminology in other species (Uher, 2008; Carter et al, 2013). To date, much research within the animal, and in particular, primate personality field has lacked clear and consistent trait classification, which may be a consequence of the variety of different methodological approaches that have been adopted (Réale et al, 2007; Carter et al, 2013).

Within primate personality research, there are three main approaches to quantifying personality (Freeman et al, 2011):

- Experimental assays seek to elicit personality-associated behaviours from subjects and record the frequency of their expression (e.g. Fairbanks et al, 2004; Carter et al, 2012).
- Behavioural coding involves analysing repeated behavioural observations of an individual to reveal patterns of repeated behaviour and the degree to which one individual differs from another in its behavioural repertoire (e.g. Seyfarth & Cheney, 2012; Garai et al, 2016).
- Subjective trait assessments involve researchers familiar with individual animals completing questionnaires, rating the degree to which subjects exhibit particular personality traits (e.g. Weiss et al, 2009; Konecná et al, 2008, 2012).

Using experimental approaches, the researcher is required to predetermine and define the personality of interest in advance. This can make it hard to quantify personality that has "functional equivalence", particularly if only a single experimental approach is used in a study (Carter et al, 2013). “Boldness” and “exploration” are the most commonly quantified personality constructs using experimental assays (Freeman et al, 2011). However, how these personalities are related to one another varies between primates species: for example, in chacma baboons (*Papio ursinus*), they are uncorrelated and require separate experimental assays (Carter et al, 2012), whereas in grey mouse lemurs (*Microcebus murinus*), boldness and exploration are highly correlated (Dammhahn & Almeling, 2012).

“Convergent construct validity” describes when two methods theoretically measuring the same element of personality generate correlated constructs, while “discriminant construct validity” describes a lack of correlation between constructs generated by two methods theoretically measuring the same construct (Carter et al, 2013). Determining the relationship between constructs is an important step in creating a comprehensive characterisation of personality within a species and is necessary before testing specific ecological hypotheses (Uher, 2008; Carter et al, 2013; 2014). Using experimental approaches in isolation makes it difficult to achieve either functional equivalence or validation of the personality constructs identified.

Subjective trait assessments have been used extensively within primatology allowing for phylogenetic comparisons and analyses of the presence and absence of factors throughout the primate family tree (Konečná et al, 2012; Adams et al, 2015). However, this methodology is inherently subjective and based on perceptions of an animal’s personality which may not reflect actual, naturally-occurring behaviour (Freeman et al, 2011). The major advantage of behavioural coding is that the method quantifies personality in a non-manipulated environment, therefore, the researcher can be confident that the personality describes “real-world” behaviour (Gosling et al, 2003). However, “interactionist” psychologists claim certain situations or environments are likely to cause individuals to behave similarly, whilst other situations will result in clear inter-individual differences (Tett & Gutterman, 2000). Therefore, long-term data collection in a range of situations or environments is required in order to identify intra-individual consistency and inter-individual variation in behaviour across multiple contexts.

Within primatology, and more broadly within animal personality research, using a range of personality assessment methods within one study remains rare (Freeman et al, 2011; but see Iwanicki & Lehmann, 2015; Garai et al, 2016). A multi-method approach has several advantages. Firstly, it allows us to compare the methodologies in terms of practicality. Secondly, it allows us to confirm that the elements of personality identified predict “actual behaviours and real-world outcomes” (Gosling et al, 2003). Finally, it generates multiple personality constructs, each of which can be examined for their relationship to one another for validation (Carter et al, 2013; Iwanicki & Lehmann, 2015) and to other individual characteristics (e.g. age, sex, rank, physiology etc.) to more completely understand how personality is manifested in a species or population (Uher, 2008).

Validation of personality constructs is rarely seen within the literature. Iwanicki & Lehmann (2015) used trait and behavioural coding to assess personality in common marmosets (*Callitrix jacchus*): four dimensions were found from trait rating (extraversion, agreeableness, conscientiousness and openness) and three from behaviour coding (agreeableness, neuroticism and perceptual sensitivity). Whilst some correlations existed between trait rating- and behavioural coding-derived constructs, each approach generated at least one construct solely identified by that methodology. Similarly, Freeman et al (2013) assessed chimpanzee personality using a "top-down, bottom-up" approach, i.e. using trait rating and behavioural coding combined once again. The authors argue that the resulting six personality constructs identified (reactivity, dominance, openness, extraversion, agreeableness and methodical) are a more representative characterisation of chimpanzee personality than previous efforts using one approach in isolation.

Currently, primate personality literature has a bias towards studies of captive populations (Freeman & Gosling, 2010). A major focus of personality research is trying to understand the evolutionary ecology of personality, i.e. understanding how intra-individual consistency and inter-individual variation in behavioural traits are maintained (Dingemanse & Reale, 2005; Wolf & Weissing, 2010). Captive primates frequently have to deal with husbandry techniques which may be stress-inducing, with subsequent implications for the welfare, health and the reproductive success of individuals (Wolfensohn & Honess, 2008). Similarly, housing conditions can create competitive and close-quarter environments, artificially increasing rates of antagonism and aggression, again with potential health and reproductive impacts (Kuhar et al, 2003). Ultimately, individual survival in captive populations relies on habituation to a unique and specific environment. This may result in a rapid depletion in behavioural trait variation within a population (McDougall et al, 2006). Artificial breeding programs may also select for captivity-friendly traits, such as docility, and can serve to accelerate homogenisation of behavioural repertoires (Archard & Braithwaite, 2010). It is evident that captive populations are potentially unhelpful subjects if we seek animal models for understanding the evolution and maintenance of personality within a species.

3.1.1 Aims

In the present study, all three methods (experimental assays, behavioural coding and subjective trait assessments) will be used to quantify personality in wild Barbary macaques (*Macaca sylvanus*). It is hoped that this chapter can provide a useful reference for future primate personality studies conducted in the *wild*, as well as providing a framework for future personality research in Barbary macaques and species with related social systems and ecology.

The overarching research question of this chapter is: "**Which personality constructs are present in wild Barbary macaques**?" To address this, personality quantification in wild Barbary macaques will be conducted usingbehavioural coding from observation data, trait rating using questionnaire-based methods, and two experimental assays (one measuring "boldness", one measuring "exploration" as defined by Réale et al, 2007). Once quantified, I will then explore the following sub- questions.

1. Do personality constructs reflect "real-world" Barbary macaque behaviour?

Personality should be reflected in "real-world" behaviours, i.e. behaviour in a non-manipulated environment (Gosling et al, 2003). Trait rating, while based on rater familiarity with subjects in the wild, is not based on behavioural data directly collected *in situ*, while experimental assays involve manipulating responses from subjects. Constructs generated from these methods can be examined for correlations with theoretically relevant behaviours collected during non-experimental behavioural observations (Freeman et al, 2013; Iwanicki & Lehmann, 2015).

2. What is the structure of Barbary macaque personality?

An aim of this chapter is to have a thorough characterisation of Barbary macaque personality, therefore, examining construct validity in relation to methodology is the final stage to deciding upon the constructs to retain and examine in greater detail*. Convergent validity* is expected to be found between the constructs identified using questionnaire trait rating and behavioural coding from observation data. Both methods aim to create a complete characterisation of personality. *Discriminant validity* is expected between the two experimental assays. The experimental assays are aiming to quantify boldness, i.e. how an individual reacts to a risky non-novel stimuli, and exploration, i.e. how an individual reacts to novel stimuli. According to the "Reinforcement Sensitivity Theory" of personality (Corr et al, 1995), boldness and exploration are two independent traits.

3.2 Methods

3.2.1 Quantifying Personality Constructs

Behavioural Coding

Behavioural data were collected using focal and scan sampling methodologies (Altmann, 1974); details of how behavioural data were collected, including definitions of behaviours, are in chapter 2. Thirty-one behaviours (table 3.1 lists behaviour variables and the type of data collected for each variable; for definitions of behaviours see table 2.8 in chapter 2) were chosen based on relevance to Barbary macaque socioecology (Hodges & Cortes, 2006; Koski, 2011; Neumann et al, 2013). Behavioural data were collected between

09/10/13-18/04/15 and divided into three time blocks based on mating season and chronological order (section 2.4.3; table 2.7). As behavioural variables were measured as frequencies and proportions, data were transformed (cubic root) and standardised (z-scores) prior to analyses (Yeo & Johnson, 2000). To examine whether individuals expressed behaviours in a consistent manner, each of the 31 behavioural variables was tested for consistency over the course of the three time blocks using an ANOVA-based measure of repeatability (R_A; section 2.9.1).

To define personality constructs, consistently expressed behavioural variables were subjected to factor analyses to identify suites of correlated variables. A mean of all behavioural variables included within a factor was used to create individual subject scores for each derived construct. Parallel analysis (generates eigenvalues expected by chance for the dataset size; components with eigenvalues greater than these chance values were retained; Horn, 1965) and skree plot visualisations were used to determine eigenvalues for and number of components. In this instance, factor analysis was preferred to principal components analyses (PCA, used in analysing trait ratings) as the aim was to identify unobservable, latent constructs accounting for correlations among the variables (Budaev, 2010; Koski, 2011).

Table 3.1: Behaviour variables used for behavioural coding. Data were divided into three time blocks, with a mean value for each variable per timeblock used in analyses (see table 2.7). For each time block, subjects would have one value per variable.

Variable	Data type
Activity	Proportion of focal observations
Self-grooming	
Grooming	
Vigilant	
Grooming density	Proportion (number of grooming partners divided by total available grooming partners)
Edge of group	Proportion of scan samples
Centre of group	
Grooming diversity	Diversity index based on grooming density (continuous real number)
Submissions	Frequency per focal observation
Retreats	
Supplant	
Self-scratch	
Body shake	
Yawn	
Tree shake	
Mounting	
Contact aggression	
Non-contact aggression	
Open mouth	
Bared teeth	
Teeth chatter	
Lip smack	
Genital touch	
Embrace	
Sandwich	
Approaches	
Neighbours 0-1m	Mean from scan samples
Neighbours 1-5m	
Neighbour 5-10m	

Trait Rating

Researchers (n=8) not involved in behavioural data collection for the current project (to avoid bias) but with experience researching the study subjects were asked to complete a questionnaire relating to the personality structure for each individual. At least two raters completed questionnaires based on their experience studying the monkeys in each of the following time periods: 2012 (March-December 2012; n = 4 raters), early 2013 (March – August 2013; n=2) and late 2013 (September – December 2013; n=2). Raters completed the questionnaire only once, i.e. each time period had raters independent from other time periods. Subjects from the Blue group were only studied and rated for the early and late 2013 time periods. Ratings were collected for 31 subjects. However, only the 27 that survived to the end of the study were included in subsequent analyses.

The questionnaire used in the present study was previously used to study another population of Barbary macaques (Konečá et al, 2012), which itself was derived from a questionnaire used to assess chimpanzee personality (King and Figueredo, 1997). The questionnaire consists of 51 items (personality traits; Appendix A4), which are rated on a 7-point scale. A score of "1" suggests the rater believes the trait is absent in the individual, whereas a score of "7" implies the rater believes the individual exhibited "extreme amounts" of the trait. Each item includes an adjective and its definition in relation to non-human primate behaviour.

Using the questionnaire data, determining personality constructs was performed through the two processes: determining which traits from the questionnaire were reliably rated (significant correlations for scores for traits for subjects from the independent raters) and identifying correlations between reliably rated traits using PCA. A mean of all traits included within a PCA-derived component was used to create individual subject scores for each derived construct.

Inter-rater reliability for item ratings was calculated using intraclass correlation coefficients (ICC; Shrout & Fleiss, 1979). Two coefficient types were used: "ICC (3, 1)", indicates the reliability of individual ratings for a trait to one another; "ICC(3,*k*)" indicates the reliability of individual ratings of a trait to a mean score for a trait based on *k* raters (Shrout & Fleiss, 1979). For items with significant inter-rater reliability ($p<0.05$ for both ICCs), mean rating values were calculated for each trait for each subject. PCAs were conducted on mean rating values for items from early and late 2013 (i.e. not 2012, when only subjects from the Green group were rated); parallel analysis and skree plot visualisations were used to determine eigenvalues for and number of components (Horn, 1965).

Experimental Assays

Experimental approaches were used to quantify the degree to which subjects expressed two personality traits: boldness, defined as responses to risky but non-novel stimuli, and exploration, defined as responses to novel but non-risky stimuli (Réale et al, 2007). The order of experiments was randomised (Bell, 2012) using a random order generator (http://www.random.org/lists). Experiments (treatments and control) were only conducted if the following conditions were met:

(i) Subject was within the group’s currently known core home range (70% of minimum convex polygon home range; data collected March-September 2013; J. Waterman, personal communication).

(ii) Time of stimulus presentation was either more than two hours after sunrise or more than two hours before sunset to minimise disturbance around sleeping sites for ethical considerations.

(iii) Following a significant disturbance (anthropogenic, inter-group encounter etc), time of stimulus presentation was delayed by 1 hour.

(iv) If a significant disturbance (e.g. inter-group encounter, human disturbance etc.) occurred during an experiment, it was abandoned.

For the boldness assay, playback experiments were conducted: subjects were presented with three audio treatments over the whole study period (09/10/2013-18/04/2015). Each treatment was composed of aggression growls and alarm barks from non-group conspecifics intended to simulate an inter-group encounter (Radford, 2008). The aggression growl treatment samples were recorded from Barbary macaques in Gibraltar, the alarm barks from wild Barbary macaques in Morocco (from the same field site, but not the subject of this study; Fischer, personal communication). The aim of the treatments was to identify how individuals responded to a threatening stimulus. A control experiment was conducted for each subject where the audio stimulus was that of a brown-necked raven (*Corvus ruficollis*), a common and frequently heard bird at the field site. The raven audio samples were recorded *in situ* from ravens found in Ifrane National Park using a Marantz PMD-660 portable recorder (Marantz America, Inc) and a Sennheiser ME66 shotgun microphone (Sennheiser Electronic Corp).

The controls were used to confirm that the responses seen in the treatments differ significantly from responses to a non-risky stimulus.

During the first field season, stimuli were broadcast using a Nagra Kudelski DSM speaker (Nagra Audio), in the second field season, a SME-AFS Portable Field Speaker (Saul Mineroff Electronics) was utilised. For both speakers, sounds were played at 55 decibels. This volume was chosen based on trying to simulate the natural occurring volumes of calls.

For each playback experiment, the speaker was placed approximately 30-50m away from the group and no more than 100m away from any one of the subjects. The speaker was kept hidden from the view of all subjects using branches or leaves. Immediately following the playing of the stimulus, researchers performed a scan of all visible subjects within their vicinity to record initial responses to the stimulus. Five response types were recorded, and assigned an ordinal value (from 2 to -2), the higher the number, the more "bold" the response:

- Agonistic (2): Subject directs aggression (bares teeth, growls, charges) towards the stimulus
- Approach (1): Subject moves more than 2m in a direction directly towards the position of the speaker
- Neutral (0): Subject appears uninfluenced by the stimulus
- Vigilance (-1): Subject is attentive to the stimulus and monitors it from a distance, possibly issuing alarm calls
- Retreat (-2): Subject moves more than 2m in a direction directly away from the position of the speaker

Following the initial scan, a 30 minute focal observation was carried out with pre-determined subjects (from a randomized order; 1-3 subjects per experiment), recording all behaviour (for definitions of behaviours, see chapter 2). Positions of these focal subjects at the time of the playback were noted and if possible marked using stones or sticks. Subsequently, a GPS was used to calculate the distance of each focal animal from the speaker at the time of the playback stimulus. As behavioural variables from these focal observations contained frequencies, durations, proportions and ordinal values, data were transformed (cubic root) and standardised (z-scores; Yeo & Johnson, 2000) prior to analysis.

For the exploration assay, novel object experiments were conducted: subjects were presented with 4 (±2) treatments (similarly sized, brightly coloured toys or household items that had not been observed occurring in the forest) and a minimum of one control (bundles of fallen branches or stones); see Appendix A5 for photographs of all treatments and an example of a control object. In order to present both treatments and controls, the objects were tied to a brown (partially camouflaged) rope and suspended from a tree, approximate 0.5m above the ground. Experiments were set up in advance and out of sight of the approaching group. When the group reached 30m from the stimulus, it was raised briefly by the observer to draw attention to the object and then left suspended approximately 0.5m above the ground. Experiments began when the first group member (including infants and juveniles) approached within 20m of the object.

Once experiments commenced, a 30 minute focal observation of the object was conducted; the observer recorded each individual (including infants and juveniles) which entered or left proximity (20m) of the object. At 2 minute intervals, the general activity (see table 2.5 for activity definitions) of all subjects (excluding infants and juveniles) that were within 20m of the object was recorded, as well as their distance from the object. During all instances of interactions with the object, the behaviours (table 2.13) and the distance of the subjects from the object were recorded. Variables were transformed (cubic root) and standardised (z-scores; Yeo & Johnson, 2000).

For both assays, exploratory PCA was applied to variables collected from treatment experiments (see table 3.2 for variables examined from treatment experiments). PCA was considered appropriate here compared to factor analysis, as the aim was to identify suites of interrelated behavioural responses as opposed to latent (occurring in a non-risky or non-novel environment) traits (Sussman et al, 2013). Parallel analysis and skree plot visualisations were used to determine eigenvalues for and the number of components (Horn, 1965). Means of all variables with salient loadings ($\geq$0.40) within a component per experiment were used as indices of response (Carter et al, 2012).

Indices derived from the assays were compared to control experiments to confirm that the indices reflect responses to either a non-novel, risky stimulus (in the case of playbacks) or a novel stimulus (in the case of novel object presentations), as opposed to a measure of general disposition. To compare the effect of experiment type (control vs treatment) on indices, a linear mixed-effects model was used with individuals as random effects and experiment type as a fixed effect; significance ($p<0.05$) was determined by F-tests of the fitted full model (Whittingham et al, 2006).

Table 3.2: Behaviour variables included in PCA analyses of experimental data.

Playback variables	Data type
Activity Self-grooming Grooming Vigilant	Proportion of focal observations
Submissive behaviours Aggressive interaction Self-scratch Body shake Yawn Mounting Aggression Affiliative behaviours Alarm bark	Frequency per focal observation
Initial response to playback	Index from -2 to +2
Novel object variables	**Data type**
Attention to stimulus Handle stimulus	Count of scans
Proximity to stimulus Vigilance	Proportion of scans

Personality Expression and Experimental Design

To examine whether experimental design affected personality expression, a number of linear mixed-effect (LME) models were created.

To avoid habituation of subjects to audio samples, multiple subjects (1-3) were observed during each playback experiment, limiting control over the precise location of each subject in relation to the speaker at the time of playing the stimulus. A LME model was used to examine if distance from the speaker and position (on the ground or in a tree/other refuge) influenced the expression of personality constructs. F-tests of fitted full models were used to identify significant variables or interactions (Whittingham et al, 2006).

For novel object experiments, individual motivation to interact with a novel object or food can be influenced by the number of conspecifics already in proximity to the object (Massen et al, 2013; Carter et al, 2014). A LME model examined if the number of other subjects in proximity to the object affected expression of personality indices. F-tests of fitted full models were used to identify significant variables or interactions (Whittingham et al, 2006).

For both experimental assays, in order to identify if there was a habituation effect over the course of the study, a LME model was used to examine if trial number affected construct score, with individual subjects as random factors. F-tests of fitted full models were used to identify if the effect of trial number was significant ($p<0.05$; Whittingham et al, 2006).

3.2.2 Determining Intra-Individual Consistency and Inter-Individual Variation in the Expression of Personality Constructs

To test whether individuals expressed the constructs identified using the three methodologies consistently, the ANOVA-based measure of repeatability (R_A) was used, with individual subjects the factorial predictors of repeatability (section 2.9.1; Nakagawa & Schielzeth, 2010). Following a randomisation procedure, p-values are calculated as the proportion of simulations that results in a random R_A greater than or equal to the observed R_A (significance $p<0.05$; i.e. more consistent than the randomisations). For behavioural coding-derived constructs, consistency was tested across the three time blocks of behavioural data collection; for the trait rating-derived constructs, consistency was tested across the three time periods the researchers completing the questionnaires worked with the subjects; for the experimental assay-derived constructs, consistency was tested between trials.

To examine inter-individual variation in the expression of construct, one way ANOVAs were performed on scores for each derived construct, comparing scores between subjects (considered significant if $p<0.05$). For trait rating- and novel object assay-derived scores, the first two scores for each subject were used to account for some subjects only having two scores for these particular constructs.

3.2.3 Relation of Behavioural Variables to Constructs Generated Outside of a Natural Setting

Percentage bend correlations (Wilcox, 1994) were used to examine the relationship between behavioural coding variables (table 3.1) and constructs generated by trait rating and experimental assays. Mean personality construct scores for each subject were compared to mean behavioural variable values for each subject, i.e. the mean of the three variable values from the three time blocks of behavioural data collection (table 3.2).

3.2.4 Testing Convergent and Discriminant Validity of Personality Constructs

Percentage bend correlations (Wilcox, 1994) were used to examine the relationship between constructs generated by behavioural coding, trait rating, and experimental assays. Mean personality construct scores for each subject were compared.

3.2.5 Determining Barbary Macaque Personality Structure

To determine the personality constructs to retain for further investigation, each derived construct must pass each of the following criteria:

C1: Expression of the construct must demonstrate temporal consistency (Sih et al, 2004); assessed using ANOVA-based measure of repeatability (R_A) with individual subjects the factorial predictors of repeatability.

C2: Expression of the construct must vary significantly between subjects (Sih et al, 2004); assessed from one-way ANOVAs of all scores comparing between subjects.

C3: The construct must reflect "real-world" behaviour, i.e. behaviour observed in a non-manipulated environment (Gosling et al, 2003); assessed by examining correlations between mean personality construct scores and mean behavioural variable values for each subject.

Using the retained constructs, a diagrammatic visualisation of Barbary macaque personality was created based on a plot of covariance between mean scores for retained personality constructs.

3.3 Results

3.3.1 Personality Constructs

Behavioural Coding

Behavioural coding generated four personality constructs which were termed Excitability_{BC}, Sociability_{BC}, Tactility_{BC} and Neuroticism_{BC} based on the following analyses.

Of the 31 behaviour variables included in the behavioural coding approach, 18 were found to be significantly consistent (see Table 3.3). Within these variables, R_A values ranged from 0.70 (Yawn) to 0.21 (Retreats and Body-shake), with a mean of 0.39. These R_A scores compare favourably with previous behavioural coding research performed in other macaque species (Neumann et al, 2013; Brent et al, 2013a) and other primates (Koski, 2011; Dammhan & Almeling, 2012; Carter et al, 2012).

The Kaiser-Meyer-Olkin measure of sampling adequacy (0.70) and Bartlett's test of sphericity ($X^2 = 813.21$, df = 153; $p<0.01$) demonstrated the remaining data, following removal of non-consistent variables, suitable for factor analysis. Parallel analysis of behavioural variables suggested four factors could be extracted. An oblique ("Promax") rotation was used, which allows for correlations between factors as factor analysis here makes no assumption about underlying structure of data (Budaev et al, 2010; Koski et al, 2011; Neumann et al, 2013). One variable was removed following the first factor analysis due to insufficient loading ($\leq$0.40; Koski, 2011) on any factor (Activity [-0.35]). The final factor analysis generated four factors which explained 66.56% of total variance. All retained variables and their loadings on factors are in table 3.4.

The first factor (accounting for 23.67% of variance) had positive loadings for variables related to dominance (mounting, open mouth), and prosocial behaviours (embrace, sandwich) as well as behaviours associated with anxiety (yawn). Therefore, this construct was called "Excitability_{BC}", a dimension of personality previously identified in Barbary macaques (Konečá et al, 2012). The second factor (accounting for 21.73% of variance) had positive loadings for behaviour variables related to being in proximity with conspecifics (time spent in centre, number of neighbours within 5-10m), so was called "Sociability_{BC}", a term used in previous macaque personality research (Weiss et al, 2011; Neumann et al, 2013; Sussman et al, 2013). The third factor contains variables related exclusively to grooming, either self- or allogrooming. Previous personality studies have related factors containing grooming variables to sociability (Neumann et al, 2013). However, the high loading for self-grooming, a solitary activity, found here suggests using different terminology. Therefore, the term "Tactility$_{BC}$" was created. The final factor (accounting for 8.57% of the variance) contained positive loadings for behaviour variables associated with being erratic or anxious (body shakes) and submissive (retreats). Such behaviour is a facet of "Neuroticism", as found in humans and chimpanzees (Weiss et al, 2009), therefore, the term "Neuroticism$_{BC}$" was applied to the factor found here.

Table 3.3: R_A and confidence intervals of behavioural variables (n = 27).

Variable				
Included in factor analysis	**R_A**	**95% confidence interval**		***P***
Yawn	0.70	0.53	0.87	<0.01
Mounting	0.52	0.30	0.75	<0.01
Edge of group	0.52	0.29	0.75	<0.01
Centre of group	0.50	0.27	0.73	<0.01
Grooming	0.48	0.25	0.72	<0.01
Genital touch	0.46	0.22	0.70	<0.01
Embrace	0.44	0.20	0.68	<0.01
Contact aggression	0.42	0.17	0.66	<0.01
Tree shake	0.40	0.16	0.65	<0.01
Open mouth	0.38	0.13	0.63	<0.01
Sandwich	0.35	0.09	0.60	<0.01
Activity	0.31	0.05	0.57	<0.01
Grooming density	0.28	0.02	0.54	0.02
Neighbours 5-10m	0.28	0.02	0.54	0.01
Neighbours 0-1m	0.25	-0.01	0.51	0.01
Self-grooming	0.22	-0.04	0.48	0.03
Retreats	0.21	-0.05	0.47	0.03
Body-shake	0.21	-0.05	0.47	0.02
Not included in factor analysis	**R_A**	**95% confidence interval**		***P***
Non-contact aggression	0.20	-0.06	0.46	0.05
Neighbours 1-5m	0.16	-0.01	0.41	0.08
Self-scratch	0.11	-0.14	0.36	0.17
Teeth chatter	0.11	-0.14	0.36	0.14
Approaches	0.10	-0.15	0.35	0.19
Grooming diversity	0.09	-0.16	0.33	0.17
Grooming evenness	0.06	-0.19	0.30	0.19
Vigilance	-0.08	-0.29	0.13	0.76
Lipsmack	-0.11	-0.31	0.09	0.85
Supplants	-0.19	-0.36	-0.02	0.97
Submissions	-0.21	-0.37	-0.05	0.98
Bare teeth	-0.24	-0.39	-0.10	0.99
Gaze	-0.35	-0.44	-0.25	>0.99

Table 3.4: Variable loadings on four extracted factors from behavioural coding; salient loadings (>0.40) are in bold. Variables which loaded significantly on more than one factor are in bold and italicised; the higher loading took precedence for determining which factor within which to include the variable.

Variable	Factor 1: $\text{Excitability}_{\text{BC}}$	Factor 2: $\text{Sociability}_{\text{BC}}$	Factor 3: $\text{Tactility}_{\text{BC}}$	Factor 4: $\text{Neuroticism}_{\text{BC}}$
Mounting	**0.76**	-0.02	-0.35	-0.26
Embrace	**0.74**	0.31	-0.15	0.12
Yawn	**0.73**	-0.27	-0.37	-0.22
Sandwich	**0.73**	0.16	0.18	-0.12
Open mouth	**0.64**	0.21	-0.21	0.25
Genital touch	**0.62**	0.06	-0.04	-0.10
Tree shake	**0.61**	-0.30	0.13	***-0.45***
Contact aggression	**0.51**	***0.44***	0.30	0.21
Central	0.16	**0.93**	0.29	0.16
Neighbours within 5-10m	-0.14	**0.71**	-0.31	-0.16
Peripheral	0.07	**-0.92**	0.03	-0.02
Allogroom	-0.25	0.29	**0.90**	-0.06
Grooming density	-0.20	0.19	**0.82**	-0.09
Neighbours within 1m	0.14	***0.47***	**0.72**	0.14
Self-groom	-0.05	-0.23	**0.60**	0.05
Body shake	-0.02	0.08	0.01	**0.84**
Retreats	-0.23	-0.08	-0.09	**0.66**

Trait Rating

Trait rating generated four personality constructs which were termed Confidence$_{TR}$, Excitability$_{TR}$, Friendliness$_{TR}$ and Introversion$_{TR}$ based on the following analyses.

Table 3.5 shows inter-rater reliability for all questionnaire items. Seven of the 51 questionnaire items were unreliably rated by raters ($p>0.05$): lazy, stingy, explorative, alert, curious, opportunistic and inventive. The ICC(3,1) coefficients for the remaining 44 items ranged from 0.13 (reckless) to 0.63 (eccentric) with a mean of 0.33. The ICC(3,k) coefficients for these items ranged from 0.51 (reckless) to 0.91 (dominance, eccentric) with a mean of 0.74. These reliability scores compare very favourably with previous trait rating research performed in macaques (Konečá et al [2012] reported mean ICC[3,1] and ICC[3,k] coefficients of 0.43 and 0.58 respectively; Adams et al [2015] reported reported mean ICC[3,1] and ICC[3,k] coefficients of 0.30 and 0.48 respectively).

Parallel analysis of ratings from early and late 2013 suggested data should be reduced to four components (Table 3.6). Varimax rotation revealed maximum interference between components 1 and 3 of 0.36, with a mean of -0.02 (Table 3.7), suggesting retention of the orthogonal components (Kim & Mueller, 1979). The four components accounted for 69.63% of variation within the dataset. Salient loadings of items on components were defined as $\geq\underline{+}0.40$ (Weiss et al, 2011; Konečá et al, 2012).

The first component (accounting for 25.64% of total variance) contained positive loadings for items such as dominant, confident and manipulative and was very similar in structure to the component "Confidence", from previous Barbary macaque research (Konečá et al, 2012; Adams et al, 2015). Therefore, the component found here was called "Confidence$_{TR}$". The second component

(19.85% of total variance) once again was similar in structure to a component found in previous Barbary macaque research, "Excitability" (Konečá et al, 2012; Adams, 2015), containing positive item loadings for disorganised, erratic and excitable, so "Excitability$_{TR}$" was used here. The third component (15.79% of total variance) bore strong similarity to a previously found component in Barbary macaques, "Friendliness" (Konečá et al, 2012; Adams, 2015). The component found in the current study, termed "Friendliness$_{TR}$", had positive item loadings for friendly, sympathetic and helpful. The final component (8.34% of total variance) contained positive item loadings for solitary and depression, and negative loadings for active and sociable. This component bears some similarity to the rhesus macaque component "Anxiety" (Adams et al, 2015). However, items were more similar to those for the human personality component "Introversion" (Gosling & John, 1999), so this term was applied here ("Introversion$_{TR}$") (Table 3.8).

Table 3.5: ICC values for questionnaire items.

Trait	ICC(3,1)	ICC(3,k)	Item variance	*F*	p-value
Dominance	0.59	0.91	0.57	10.92	<0.01
Eccentric	0.63	0.91	2.57	13.39	<0.01
Irritability	0.54	0.89	1.26	9.39	<0.01
Submissive	0.50	0.88	3.61	7.80	<0.01
Solitary	0.50	0.87	1.61	8.50	<0.01
Popular	0.47	0.86	1.34	10.10	<0.01
Timid	0.46	0.85	1.70	6.63	<0.01
Equable	0.46	0.85	0.57	6.78	<0.01
Depressed	0.44	0.85	2.97	6.59	<0.01
Insecure	0.43	0.84	4.74	6.47	<0.01
Independent	0.42	0.83	1.50	5.91	<0.01
Disorganised	0.45	0.83	1.21	6.96	<0.01
Sociable	0.41	0.83	1.62	7.39	<0.01
Fearful	0.41	0.83	1.40	5.86	<0.01
Tense	0.40	0.82	2.55	6.85	<0.01
Protective	0.38	0.81	0.48	5.52	<0.01
Helpful	0.36	0.80	0.34	6.95	<0.01
Erratic	0.36	0.80	2.06	5.45	<0.01
Aggressive	0.35	0.79	1.94	5.52	<0.01
Confidence	0.34	0.78	1.41	4.71	<0.01
Gentle	0.31	0.76	1.27	4.67	<0.01
Affectionate	0.30	0.75	0.71	5.13	<0.01
Excitable	0.28	0.73	0.18	3.73	<0.01
Intelligence	0.27	0.73	1.40	4.39	<0.01
Consistent	0.28	0.73	0.76	4.27	<0.01
Impulsive	0.27	0.72	1.75	3.78	<0.01
Friendly	0.27	0.72	0.76	4.72	<0.01
Manipulative	0.27	0.72	1.60	3.98	<0.01
Playful	0.27	0.72	0.30	5.50	<0.01
Persistent	0.26	0.71	0.52	3.60	<0.01
Sympathetic	0.25	0.70	0.57	5.21	<0.01
Socially playful	0.24	0.69	0.88	4.81	<0.01
Permissive	0.24	0.69	1.33	3.30	<0.01
Conventional	0.23	0.67	0.78	3.68	<0.01
Bullying	0.22	0.66	1.75	3.17	<0.01
Patient	0.20	0.64	0.30	2.92	<0.01
Sensitive	0.19	0.62	0.79	3.46	<0.01
Unemotional	0.18	0.60	0.26	2.50	<0.01
Active	0.18	0.60	0.59	3.46	<0.01
Selective	0.17	0.60	1.94	2.57	0.01
Jealous	0.16	0.58	1.19	2.29	0.02
Assertive	0.15	0.54	0.54	2.23	0.03

Cautious	0.13	0.52	1.43	2.06	0.04
Reckless	0.13	0.51	1.40	2.03	0.05
Stingy*	0.02	0.07	3.29	1.08	0.38
Lazy*	0.06	0.21	0.13	1.33	0.16
Explorative*	-0.06	-0.27	6.41	0.76	0.79
Alert*	0.00	0.00	4.02	1.00	0.48
Curious*	-0.04	-0.19	3.84	0.80	0.75
Opportunistic*	-0.01	-0.05	3.46	0.93	0.57
Inventive*	-0.05	-0.25	0.32	0.71	0.85

* Items marked were not significantly reliably rated (p>0.05).

Table 3.6: Eigenvalues from parallel analysis and actual analysis of ratings from summer and winter 2013.

Component	Adjusted eigenvalue - parallel	Adjusted eigenvalue – actual	% of variance	Cumulative % of variance
1	10.99	13.10	29.76	29.76
2	7.54	9.37	21.29	51.05
3	3.19	4.82	10.95	62.00
4	1.90	3.36	7.63	69.63

Table 3.7: Correlations among components after promax rotation.

Component	1	2	3	Mean
1				
2	-0.03			
3	0.36	-0.22		
4	-0.21	-0.06	-0.16	-0.20

Table 3.8: Item loadings for components from trait ratings; salient loadings (>0.40) are in bold. Variables which loaded significantly on more than one factor are in bold and italicised; the higher loading took precedence for determining which factor within which to include the variable.

Variable	Component 1: Confidence$_{TR}$	Component 2: Excitability$_{TR}$	Component 3: Friendliness$_{TR}$	Component 4: Introversion$_{TR}$
Dominant	**0.92**	-0.18	0.12	-0.11
Dependent	**-0.91**	0.08	-0.11	-0.06
Confident	**0.89**	-0.12	0.23	-0.12
Subordinate	**-0.86**	0.03	0.03	0.07
Timid	**-0.86**	0.01	-0.21	0.12
Fearful	**-0.80**	0.13	-0.29	0.07
Manipulative	**0.80**	0.16	0.06	-0.03
Aggressive	**0.77**	0.38	-0.17	-0.06
Independent	**0.77**	0.12	0.08	***0.45***
Persistent	**0.75**	0.19	0.09	-0.05
Popular	**0.73**	-0.16	0.34	-0.28
Protective	**0.73**	-0.11	0.37	0.28
Intelligent	**0.72**	-0.18	0.14	-0.22
Bullying	**0.60**	***0.48***	-0.33	-0.18
Cautious	**-0.55**	***-0.53***	-0.14	0.27
Irritable	**0.52**	***0.41***	-0.40	0.11
Selective	**0.51**	***-0.45***	-0.22	-0.14
Disorganised	-0.08	**0.90**	0.07	0.21
Excitable	0.05	**0.82**	-0.09	-0.22
Impulsive	-0.02	**0.79**	-0.20	-0.16
Reckless	0.39	**0.77**	0.03	-0.01
Erratic	-0.19	**0.77**	-0.13	0.03
Predictable	0.27	**-0.72**	***0.40***	-0.17
Playful	0.04	**0.66**	0.52	-0.01
Conventional	-0.05	**-0.65**	0.11	-0.26
Unemotional	0.13	**-0.64**	0.28	0.21
Eccentric	-0.05	**0.61**	0.21	***0.42***
Stable	***0.46***	**-0.59**	***0.47***	-0.07
Defiant	***0.48***	**0.55**	0.10	-0.06
Jealous	0.11	**0.52**	-0.24	-0.04
Patient	0.36	**-0.51**	***0.46***	0.23
Affectionate	0.13	0.14	**0.85**	-0.07
Sympathetic	0.17	-0.17	**0.85**	-0.13
Friendly	-0.03	-0.12	**0.82**	-0.33
Gentle	-0.06	-0.26	**0.80**	0.27
Helpful	0.24	-0.26	**0.77**	-0.13
Social play	0.23	0.35	**0.71**	-0.14

Tense	***-0.46***	0.13	**-0.51**	0.14
Permissive	0.28	-0.37	**0.51**	0.36
Sensitive	0.07	***-0.42***	**0.44**	-0.12
Solitary	0.00	0.06	-0.14	**0.86**
Depressed	-0.35	0.20	-0.24	**0.74**
Active	0.16	0.42	0.05	**-0.68**
Sociable	0.22	-0.05	***0.57***	**-0.65**

Experimental assays

The playback experiments generated four personality constructs which were termed Boldness$_{EXP}$, Sustained Sociability$_{EXP}$, Brief Sociability$_{EXP}$ and Anxiety$_{EXP}$. The novel object experiments generated two personality constructs which were termed Visual Exploration$_{EXP}$ and Physical Exploration$_{EXP}$.

Twenty-seven subjects were each subjected to three playback treatment experiments and one control experiment. Three treatment experiments were performed when the subject exceeded 100m from the speaker and was thought not to hear the sound played. Analyses were performed both with and without these observations included. For the exploration assays, 27 subjects participated (entered into proximity with the object) in one control experiment and a mean of 4.2 (±1.2) treatment experiments.

Parallel analysis of playback responses suggested data should be reduced to four components (Table 3.9). Varimax rotation revealed maximum interference between components 1 and 3 of 0.20, with a mean of 0.09 (Table 3.10), suggesting retention of the orthogonal components (Kim & Mueller, 1979). The four components accounted for 47.20% of variance in responses to the treatment playbacks. Salient loadings of items on components were defined as ≥±0.40 (Weiss et al, 2011; Konečá et al, 2012). Five variables did not load saliently onto any of the components (body shake, present for groom, yawn, submissions and initial playback response).

Table 3.11 contains the loadings for variables on the components. The first component (accounting for 12.89% of total variance) contained positive loadings for variables related to dominance, namely aggression and supplants, as well as more prosocial behaviours, namely approaches and affiliative sounds. The component's structure bore similarity to the "Confidence" component identified in previous Barbary macaque research (Konečá et al, 2012). However, in the context here, i.e. following a playback treatment, this component was named "Boldness$_{EXP}$", implying a positive and non-fearful response to a risky situation (Réale et al, 2007). The second and third components contained variables related to sociality. The second component (11.28% of total variance) contained variables related to sustained contact sociality (grooming and proportion of time spent in proximity with others), while the third component (10.81% of total variance) contained variables related to brief encounter social bonding (affiliative contact and mounting"). Both components appeared to be elements of general "Sociability", a behavioural response to experimental assays identified in other macaque species (Sussman et al, 2013), and were thus named "Sustained Sociability$_{EXP}$" and "Brief Sociability$_{EXP}$". The final component (10.55% of total variance) contained behavioural variables suggesting negative, anxious and fearful responses to the playback treatments (scratches, self-grooming and vigilant), and thus was termed "Anxiety$_{EXP}$", a response to experimental assays seen in other macaque and primate species (Carter et al, 2012; Neumann et al, 2013; Sussman et al , 2013).

Table 3.9: Eigenvalues from parallel analysis and actual analysis of behavioural responses to playback treatments.

Component	Adjusted eigenvalue - parallel	Adjusted eigenvalue – actual	% of variance	Cumulative % of variance
1	2.10	3.08	16.23	16.23
2	1.54	2.30	12.11	28.34
3	1.25	1.87	9.84	38.17
4	1.22	1.72	9.03	47.20

Table 3.10: Correlations among components after promax rotation.

Component	1	2	3	Mean
1				
2	0.18			
3	0.20	0.01		
4	0.03	0.00	0.13	0.09

Table 3.11: Variable loadings for the four components from playback treatment responses; salient loadings (>0.40) are in bold. Variables which loaded significantly on more than one factor are in bold and italicised; the higher loading took precedence for determining which factor within which to include the variable.

Variable	Component 1: $\text{Boldness}_{\text{EXP}}$	Component 2: Sustained $\text{Sociability}_{\text{EXP}}$	Component 3: Brief $\text{Sociability}_{\text{EXP}}$	Component 4: $\text{Anxiety}_{\text{EXP}}$
Approaches	**0.75**	0.18	0.30	-0.02
Affiliative sound	**0.70**	0.22	-0.20	-0.01
Supplant	**0.64**	-0.36	-0.16	-0.20
Aggression	**0.61**	0.24	0.23	0.25
Gaze	**0.40**	0.01	-0.09	0.16
Allogrooming	-0.14	**0.79**	-0.14	-0.08
Proximity with conspecifics	0.30	**0.78**	0.11	-0.15
Activity	0.35	**0.65**	0.11	0.25
Coalitions	-0.05	0.03	**0.84**	0.01
Mounting	0.20	-0.01	**0.81**	0.10
Affiliative contact	0.39	0.02	**0.55**	-0.21
Scratch	0.11	0.01	0.08	**0.81**
Self-grooming	-0.15	0.16	-0.14	**0.73**
Vigilant	-0.02	-0.38	0.13	**0.68**

Parallel analysis of novel object treatments suggested the data should be reduced to two components (Table 3.12). Varimax rotation revealed interference between the two components of -0.01, suggested retention of the orthogonal components (Kim & Mueller, 1979). The two components accounted for 63.25% of variance in responses to novel object treatments. Salient loadings of items on components were defined as ≥±0.40 (Weiss et al, 2011; Konečá et al, 2012).

Table 3.13 contains the loadings for variables on components. The first component contained positive loadings for "attention to the stimulus" and "vigilance in proximity of object" and thus was termed "Visual Exploration$_{EXP}$", accounting for 32.92% of variance. The second component contained positive loadings for "handle object" and "proportion of scans in proximity with object" and thus was termed "Physical Exploration$_{EXP}$", accounting for 30.33% of variance.

Table 3.12: Eigenvalues from parallel analysis and actual analysis of behavioural responses to novel object treatments.

Component	Adjusted eigenvalue - parallel	Adjusted eigenvalue – actual	% of Variance	Cumulative % of variance
1	1.10	1.32	32.92	32.92
2	1.16	1.21	30.33	63.25

Table 3.13: Variable loadings for the two extracted components from novel object treatment responses; salient loadings (>0.40) are in bold.

Variable	Component 1: Visual Exploration$_{EXP}$	Component 2: Physical Exploration$_{EXP}$
Attention to stimulus	**0.82**	0.12
Vigilant in proximity of stimulus	**0.80**	-0.13
Handle stimulus	0.08	**0.79**
Scans spent in proximity of stimulus	-0.09	**0.75**

Two of the playback experiment-derived constructs, Boldness$_{EXP}$ and Anxiety$_{EXP}$ were expressed higher in treatment experiments compared to control experiments, suggesting these personality constructs formed a specific reaction to non-novel but threatening stimulus. Significant differences were observed between scores in treatments and controls for the Boldness$_{EXP}$ (F = 14.30; df = 1; $p<0.01$) and Anxiety$_{EXP}$ (F = 29.88; df = 1; $p<0.01$) constructs (figure 3.1). Non-significant differences between controls and treatments were seen for scores for the Sustained Sociability$_{EXP}$ (F = 0.71; df = 1; $p = 0.40$) and Brief Sociability$_{EXP}$ (F = 0.05; df = 1; $p = 0.82$) constructs (figure 3.2).

Of the two novel object experiment-derived constructs, only Visual Exploration$_{EXP}$ was expressed more highly in treatment experiment compared to control experiments. Significant differences were seen between the control and treatment experiments for scores of Visual Exploration$_{EXP}$ (F = 23.22; df = 1; $p<0.01$), but not Physical Exploration$_{EXP}$ (F = 0.28; df = 1; $p = 0.59$; figure 3.3).

Experimental design variables affected the expression of two playback experiment-derived constructs (table 3.14). Whether or not subjects were on the ground at the time of the stimulus playback was found to affect $\text{Boldness}_{\text{EXP}}$ scores in treatment experiments; individuals off the ground scored higher than individuals on the ground (F = 14.70; df = 46; $p<0.01$). The distance of the subject from the speaker at the time of the playback was found to affect Sustained $\text{Sociability}_{\text{EXP}}$ scores; those further away scored lower than those closer to the speaker (F = 5.78; df = 46; p = 0.02). The other playback experiment-derived constructs were not affected by these variables. Figure 3.4 illustrates how $\text{Boldness}_{\text{EXP}}$ and Sustained $\text{Sociability}_{\text{EXP}}$ were affected by experiment design variables.

In the novel object experiments, neither Visual $\text{Exploration}_{\text{EXP}}$ nor Physical $\text{Exploration}_{\text{EXP}}$ scores were affected by the number of conspecifics in proximity with the object when the subject entered proximity with the object (table 3.15).

There was no relationship between trial number and any experiment-derived construct score, with the exception of Physical $\text{Exploration}_{\text{EXP}}$ (table 3.16). For this construct, scores decreased with trial number.

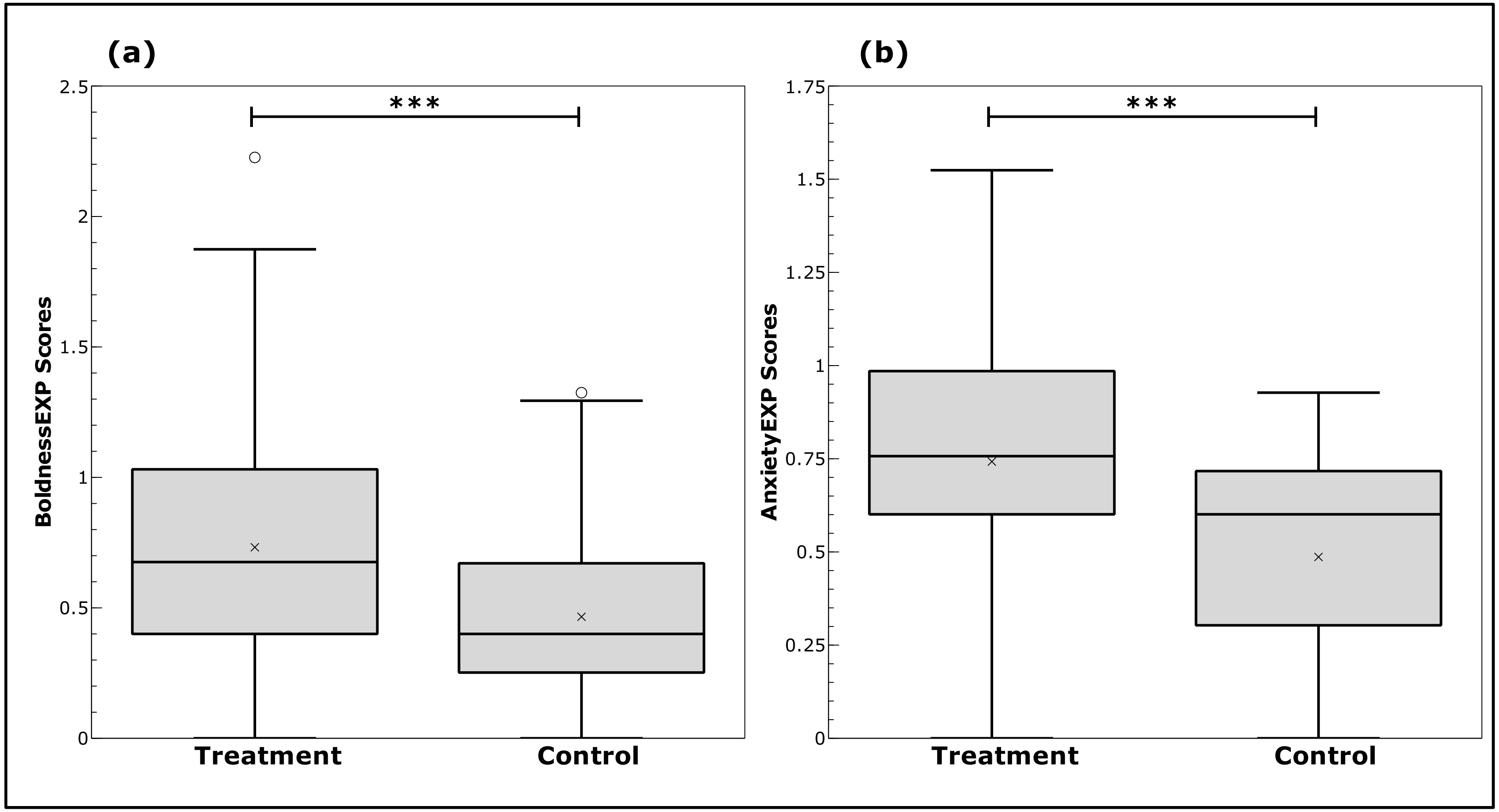


Figure 3.1: Median values (central line in box) and 25% percentiles (edge of boxes) of personality scores in playback treatment and control experiments for both (a) Boldness$_{EXP}$ and (b) Anxiety$_{EXP}$ (n=81 for treatments; n=27 for controls). Crosses represent means and circles represent outliers.

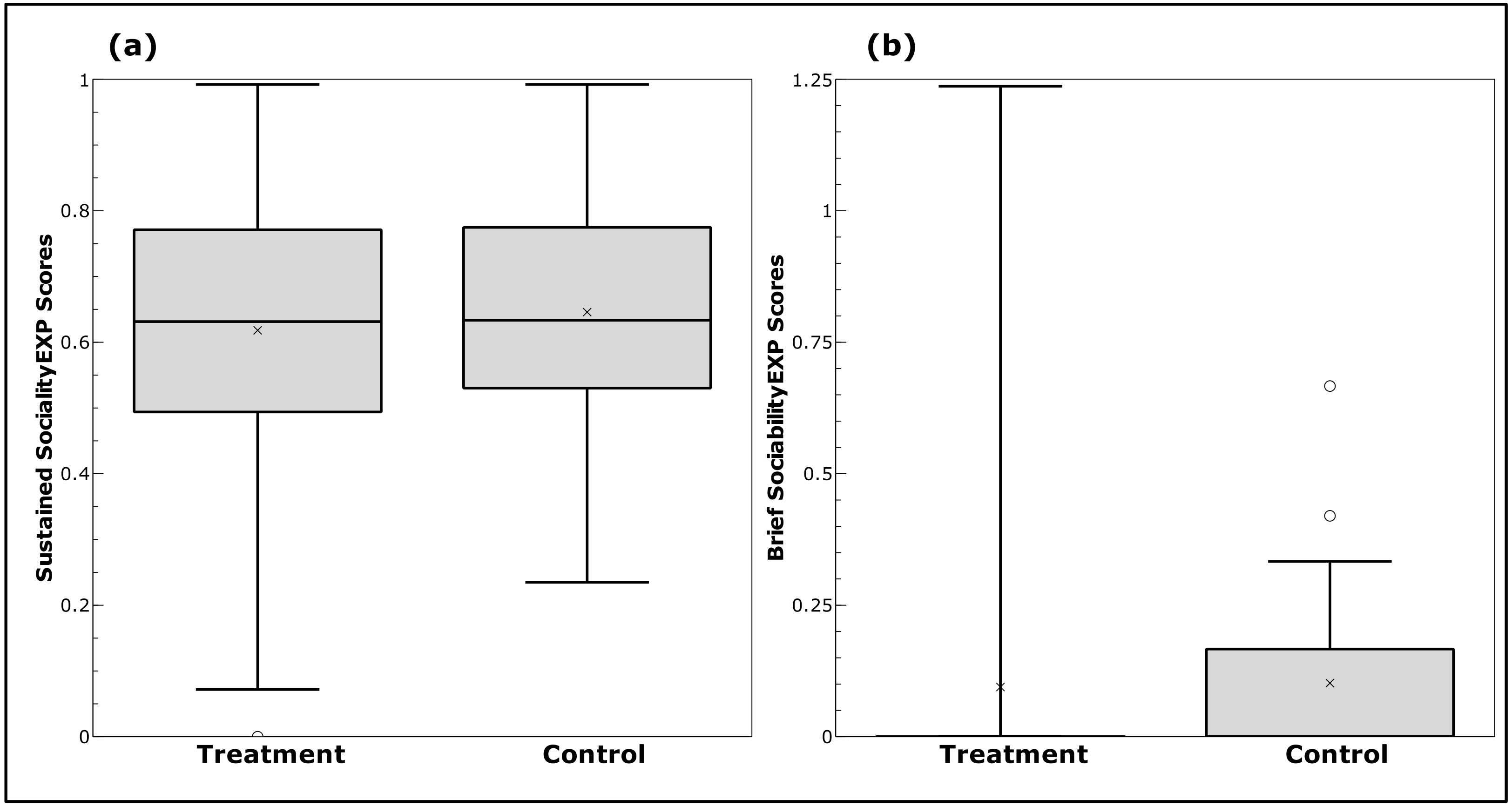


Figure 3.2: Median values (central line in box) and 25% percentiles (edge of boxes) of personality scores in playback treatment and control experiments for both (a) Sustained Sociability$_{\text{EXP}}$ and (b) Brief Sociability$_{\text{EXP}}$ (n=81 for treatments; n=27 for controls). Crosses represent means and circles represent outliers.

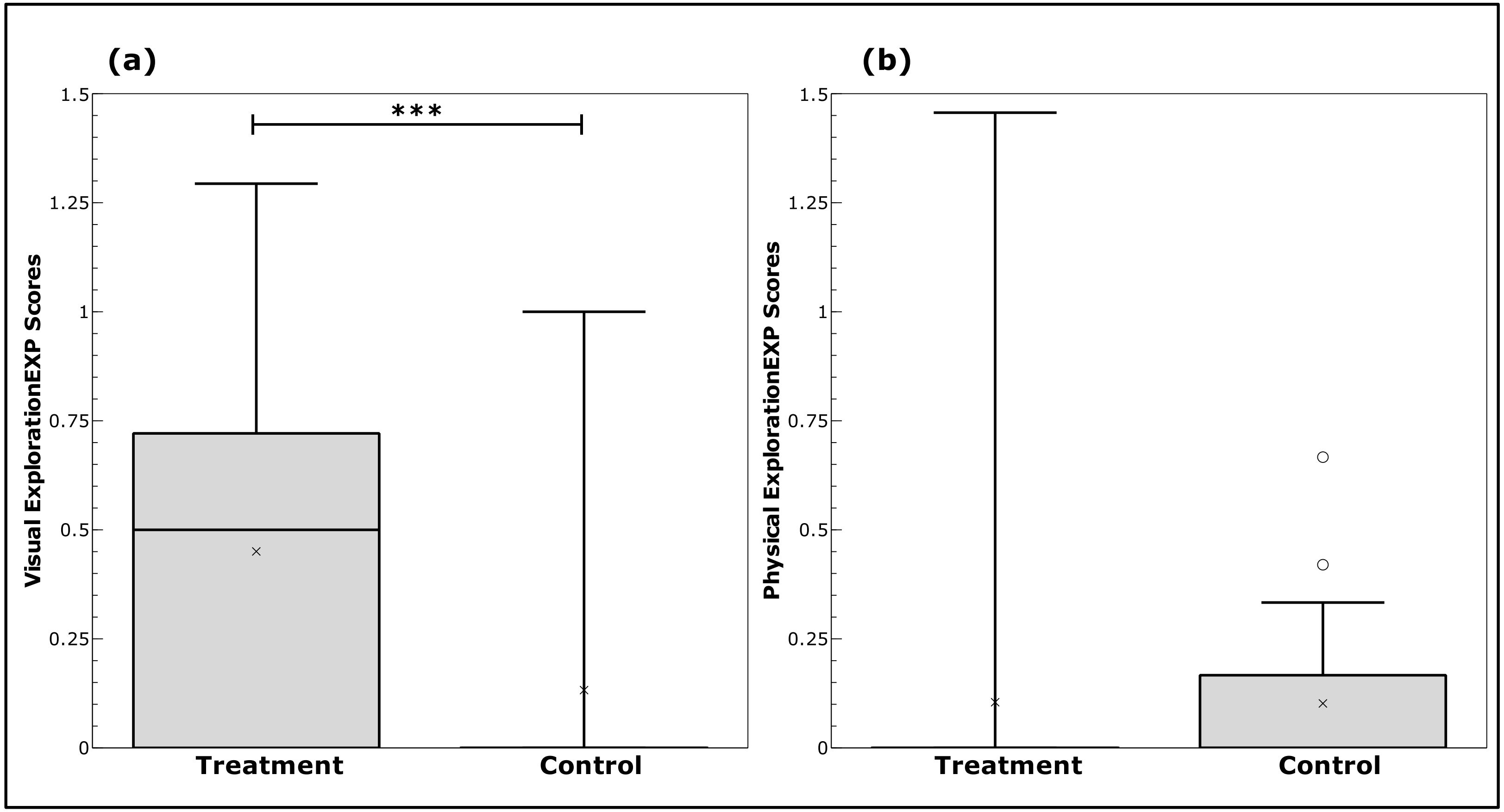


Figure 3.3: Median values (central line in box) and 25% percentiles (edge of boxes) of personality scores in playback treatment and control experiments for both (a) Visual Exploration$_{EXP}$ and (b) Physical Exploration$_{EXP}$ (n=114 for treatments; n=27 for controls). Crosses represent means and circles represent outliers.

Table 3.14: Results of linear-mixed effect models examining relationships between design variables and the expression of playback experiment-derived personality constructs. Each construct was analysed in a separate model. Significant relationships are in bold.

Construct	Variable	*β*	SE	*F*	*p*
Boldness$_{EXP}$	Intercept	0.58	0.22		
	On ground	**0.20**	**0.35**	**12.85**	**<0.01**
	Distance from speaker	<0.01	<0.01	0.14	0.71
	Ground + Distance from speaker	<0.01	0.01	0.17	0.68
Anxiety$_{EXP}$	Intercept	0.82	0.16		
	On ground	0.03	<0.01	3.46	0.07
	Distance from speaker	<-0.01	0.26	0.17	0.68
	Ground + Distance from speaker	<0.01	<0.01	0.15	0.70
Brief Sociability$_{EXP}$	Intercept	0.14	0.11		
	On ground	-0.08	0.18	0.02	0.90
	Distance from speaker	<-0.01	<0.01	0.04	0.84
	Ground + Distance from speaker	<0.01	<0.01	0.20	0.66
Sustained Sociability$_{EXP}$	Intercept	0.86	0.11		
	On ground	-0.16	0.18	0.91	0.34
	Distance from speaker	**<-0.01**	**<0.01**	**5.78**	**0.02**
	Ground + Distance from speaker	<-0.01	<0.01	1.44	0.23

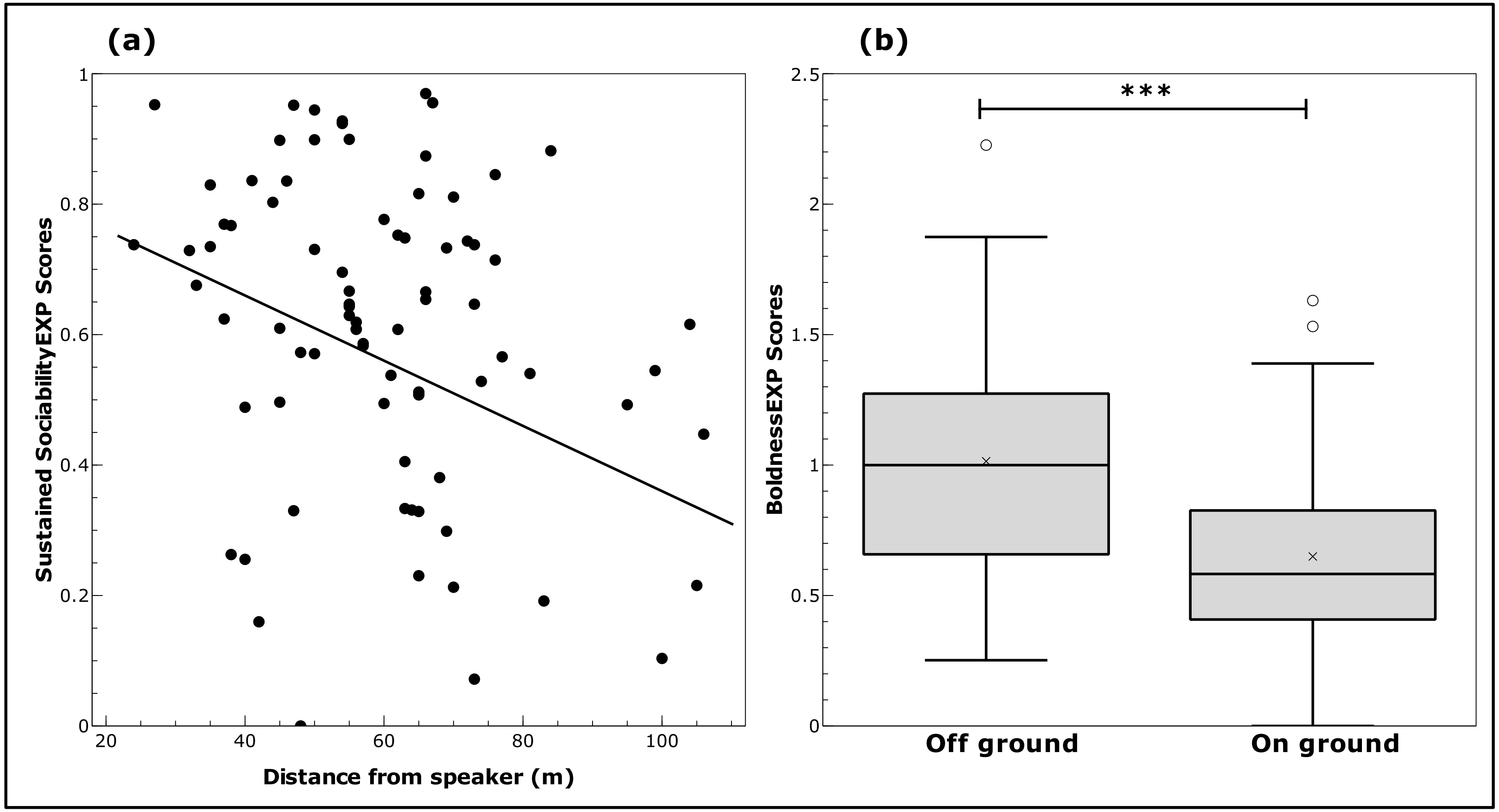


Figure 3.4: Relationships between experiment design variables and the expression of playback experiment-derived constructs; (a) illustrates relationship between Sustained Sociability$_{EXP}$ scores and distance from speaker at the time of playback stimuli (n=81); (b) median values (central line in box) and 25% percentiles (edge of boxes) of Boldness$_{EXP}$ scores when subjects were on (n=39) or off the ground (n=42) at the time of the playback stimuli. Crosses represent means and circles represent outliers.

Table 3.15: Results of linear-mixed effect model examining whether the number of conspecifics in proximity to the novel object when the subject entered proximity with the object was related to variation in the expression of novel object experiment-derived personality constructs.

Construct	Variable	β	SE	*F*	*p*
Visual Exploration$_{EXP}$	Intercept	0.49	0.07		
	Number of conspecifics	0.02	0.03	0.37	0.54
Physical Exploration$_{EXP}$	Intercept	0.10	0.04		
	Number of conspecifics	0.01	0.02	0.18	0.68

Table 3.16: Results of linear-mixed effect models examining the relationship between experiment trial number and the scores for experiment-derived personality constructs. Significant effects are in bold.

Construct	β	SE	F	*p*
Intercept	1.94	0.37		
Anxiety$_{EXP}$	0.25	0.29	1.17	0.28
Boldness$_{EXP}$	0.27	0.21	0.68	0.42
Brief Sociability$_{EXP}$	-0.66	0.44	2.33	0.13
Sustain Sociability$_{EXP}$	-0.49	0.40	1.49	0.22
Intercept	2.67	0.23		
Visual Exploration$_{EXP}$	0.56	0.33	2.98	0.09
Physical Exploration$_{EXP}$	**-1.70**	**0.59**	**8.18**	**0.01**

3.3.2 Inter-Individual Variation and Intra-Individual Consistency in the Expression of Personality Constructs

Intra-Individual Consistency

Of the 14 personality constructs identified using the three methodologies, eight were significantly consistently expressed across their respective time periods (i.e. across the three time blocks for behavioural coding, across trials for experimental assays and across the years researchers completing the questionnaires worked with the subjects; table 3.17).

Subjects demonstrated significantly consistent scores for the constructs derived from behavioural coding with the exception of Neuroticism_{BC} (R_A = -0.02; p = 0.59). R_A ranged from -0.02 for Neuroticism_{BC} to 0.70 for Excitability_{BC}, with a mean of 0.44. Visual inspection of intra-individual consistency scores for Neuroticism_{BC} suggested two individuals (CON and TIM) were the cause of low consistency for this construct. However, even when these individuals were removed from the dataset, R_A for Neuroticism_{BC} remained non-significant (R_A = 0.12; p =0.23).

Subjects demonstrated significant consistency for all personality constructs derived from trait ratings. R_A ranged from 0.57 for "Friendliness_{TR}" to 0.82 for "Confidence_{TR}", with a mean of 0.68.

The only experimental assay-derived construct in which subjects demonstrated significantly consistent scores across trials was "Boldness_{EXP}" (R_A = 0.22, p=0.04). Visual inspection of intra-individual consistency scores for Anxiety_{EXP} suggested four individuals (ANN, KER, ELI and PEN) were the cause of low repeatability for this construct. However, following the removal of these individuals from the analysis, consistency remained non-significant (R_A = 0.14, p<0.13). R_A for "Visual Exploration$_{EXP}$" approached significance ($R_A = 0.09$, $p = 0.08$)

Table 3.17: Testing of consistency of personality constructs using ANOVA-based measure (R_A). Statistical significance implies that subjects had consistent scores for the personality constructs; indicated by bold text.

Construct	R_A	95% Confidence Interval		p
Excitability$_{BC}$	**0.70**	**0.54**	**0.87**	**<0.01**
Sociability$_{BC}$	**0.46**	**0.22**	**0.70**	**<0.01**
Tactility$_{BC}$	**0.59**	**0.39**	**0.79**	**<0.01**
Neuroticism$_{BC}$	-0.02	-0.25	0.20	0.59
Confidence$_{TR}$	**0.82**	**0.70**	**0.94**	**<0.01**
Excitability$_{TR}$	**0.68**	**0.49**	**0.87**	**<0.01**
Friendliness$_{TR}$	**0.57**	**0.33**	**0.80**	**<0.01**
Introversion$_{TR}$	**0.64**	**0.44**	**0.85**	**<0.01**
Anxiety$_{EXP}$	0.08	-0.17	0.33	0.23
Boldness$_{EXP}$	**0.22**	**-0.03**	**0.48**	**0.04**
Brief Sociability$_{EXP}$	-0.04	-0.23	0.23	0.47
Sustain Sociability$_{EXP}$	0.15	-0.10	0.41	0.10
Visual Exploration$_{EXP}$	0.09	-0.01	0.28	0.08
Physical Exploration$_{EXP}$	-0.02	-0.17	0.13	0.58

Inter-Individual Variation

One way ANOVAs revealed significant variation between subjects for Excitability$_{BC}$, Sociability$_{BC}$, Tactility$_{BC}$, Confidence$_{TR}$, Excitability$_{TR}$, Friendliness$_{TR}$, Introversion$_{TR}$, Boldness$_{EXP}$ and Visual Exploration$_{EXP}$ (table 3.18). Figures 3.5 to 3.11 illustrate individual scores of subjects for each personality construct.

Table 3.18: Results of one-way ANOVAs examining variation among subjects in scores for personality constructs. Personality scores which varied between subjects are in bold.

Factor	df	F	*p*
Excitability$_{BC}$	**26,54**	**7.17**	**<0.01**
Sociability$_{BC}$	**26,54**	**3.12**	**<0.01**
Tactility$_{BC}$	**26,54**	**4.63**	**<0.01**
Neuroticism$_{BC}$	26,54	0.88	0.63
Confidence$_{TR}$	**26,41**	**3.12**	**<0.01**
Excitability$_{TR}$	**26,41**	**2.66**	**<0.01**
Friendliness$_{TR}$	**26,41**	**3.02**	**<0.01**
Introversion$_{TR}$	**26,41**	**3.55**	**<0.01**
Anxiety$_{EXP}$	26,54	1.27	0.23
Boldness$_{EXP}$	**26,54**	**2.61**	**0.04**
Brief Sociability$_{EXP}$	26,54	1.40	0.15
Sustained Sociability$_{EXP}$	26,54	1.36	0.17
Visual Exploration$_{EXP}$	**26,86**	**1.99**	**<0.05**
Physical Exploration$_{EXP}$	26,86	0.53	0.96

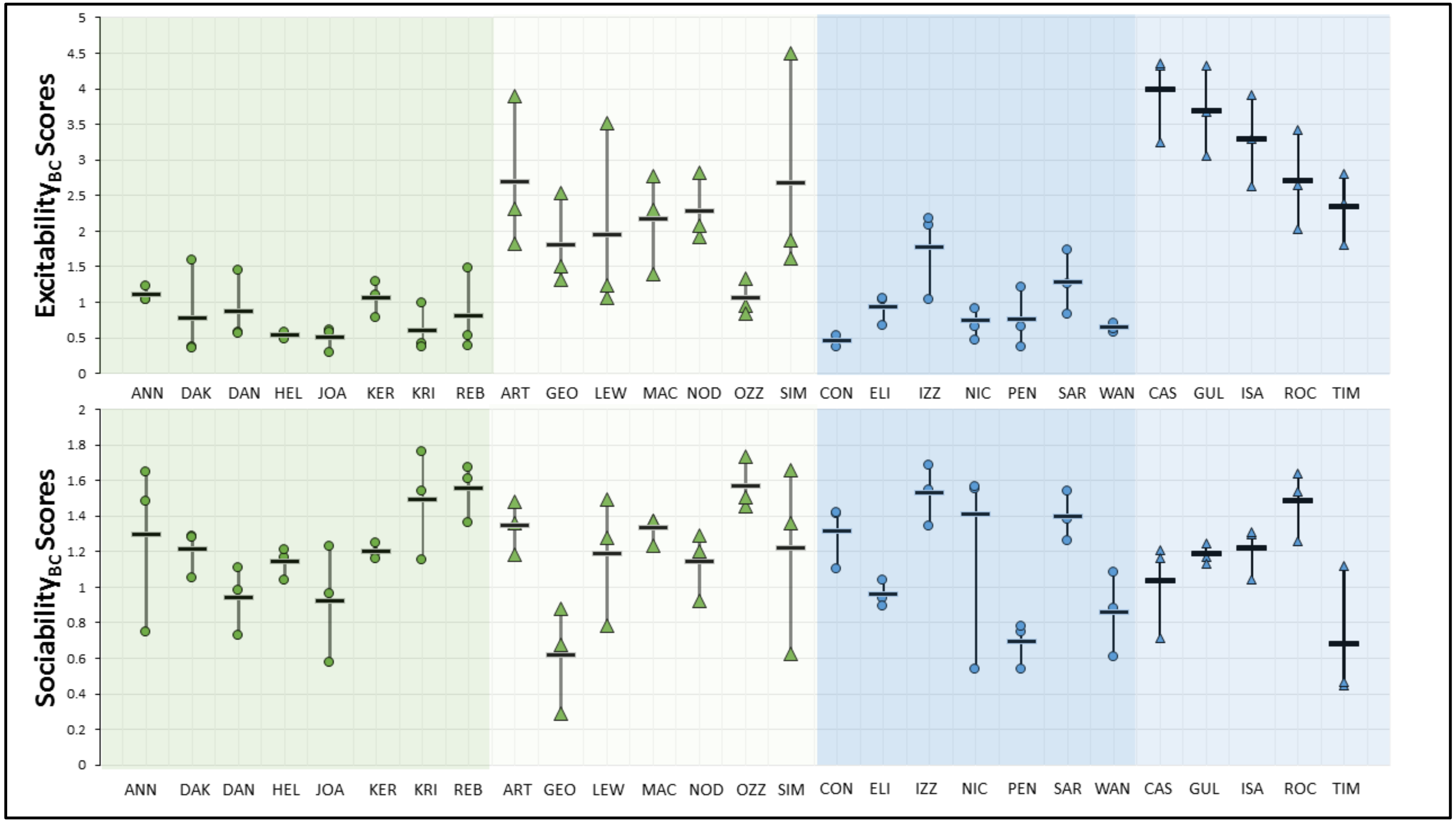


Figure 3.5: Excitability$_{BC}$ and Sociability$_{BC}$ scores for subjects (n=81). Each plot represents an individual score by a subject, the black bars represent mean score for a subject. Subjects are ordered by group (Green and Blue Group coloured green and blue respectively) and sex (females represented by ●; males represented by ▲).

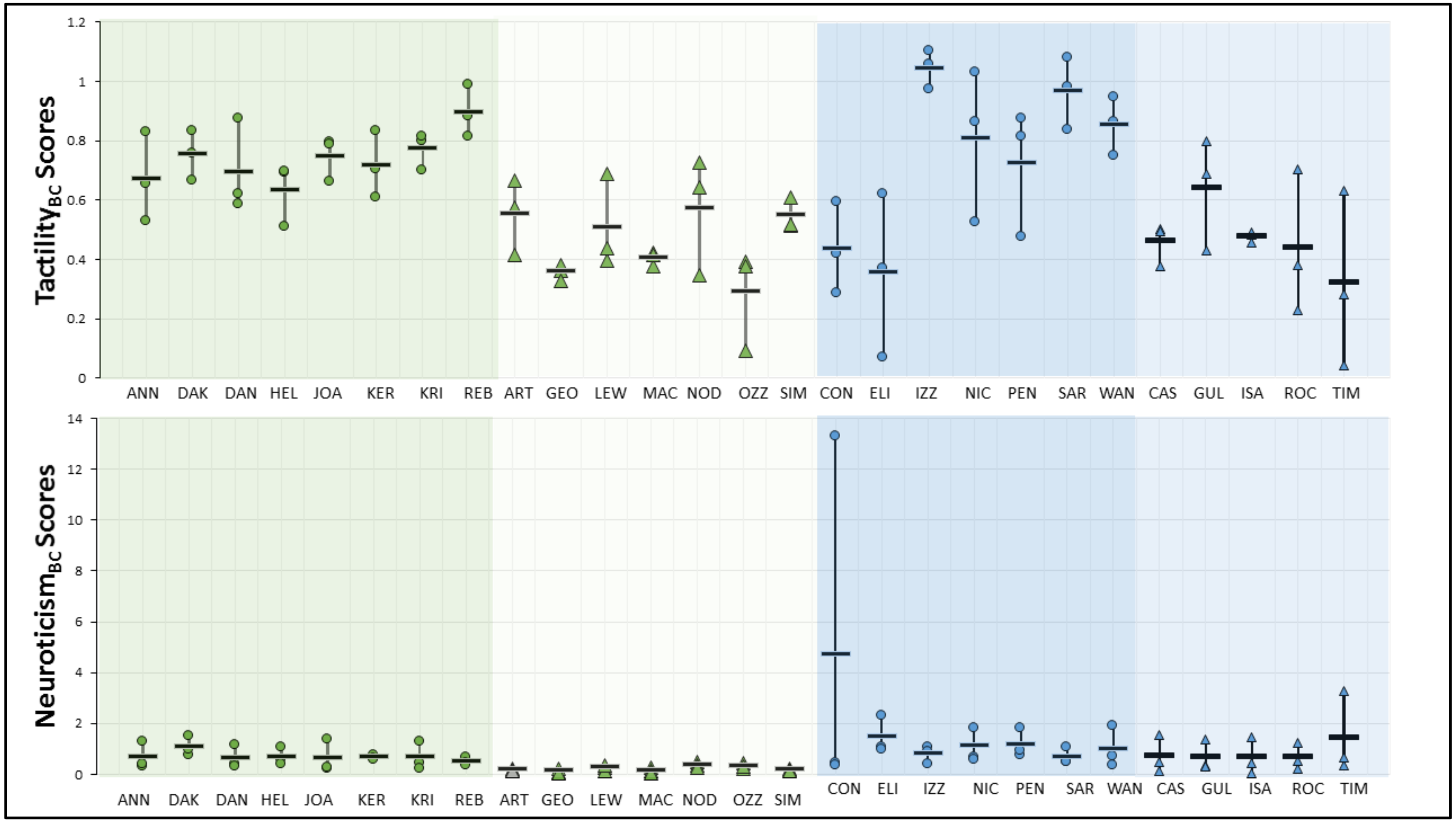


Figure 3.6: Tactility$_{BC}$ and Neuroticism$_{BC}$ scores for subjects (n=81). Each plot represents an individual score by a subject, the black bars represent mean score for a subject. Subjects are ordered by group (Green and Blue Group coloured green and blue respectively) and sex (females represented by ●; males represented by ▲).

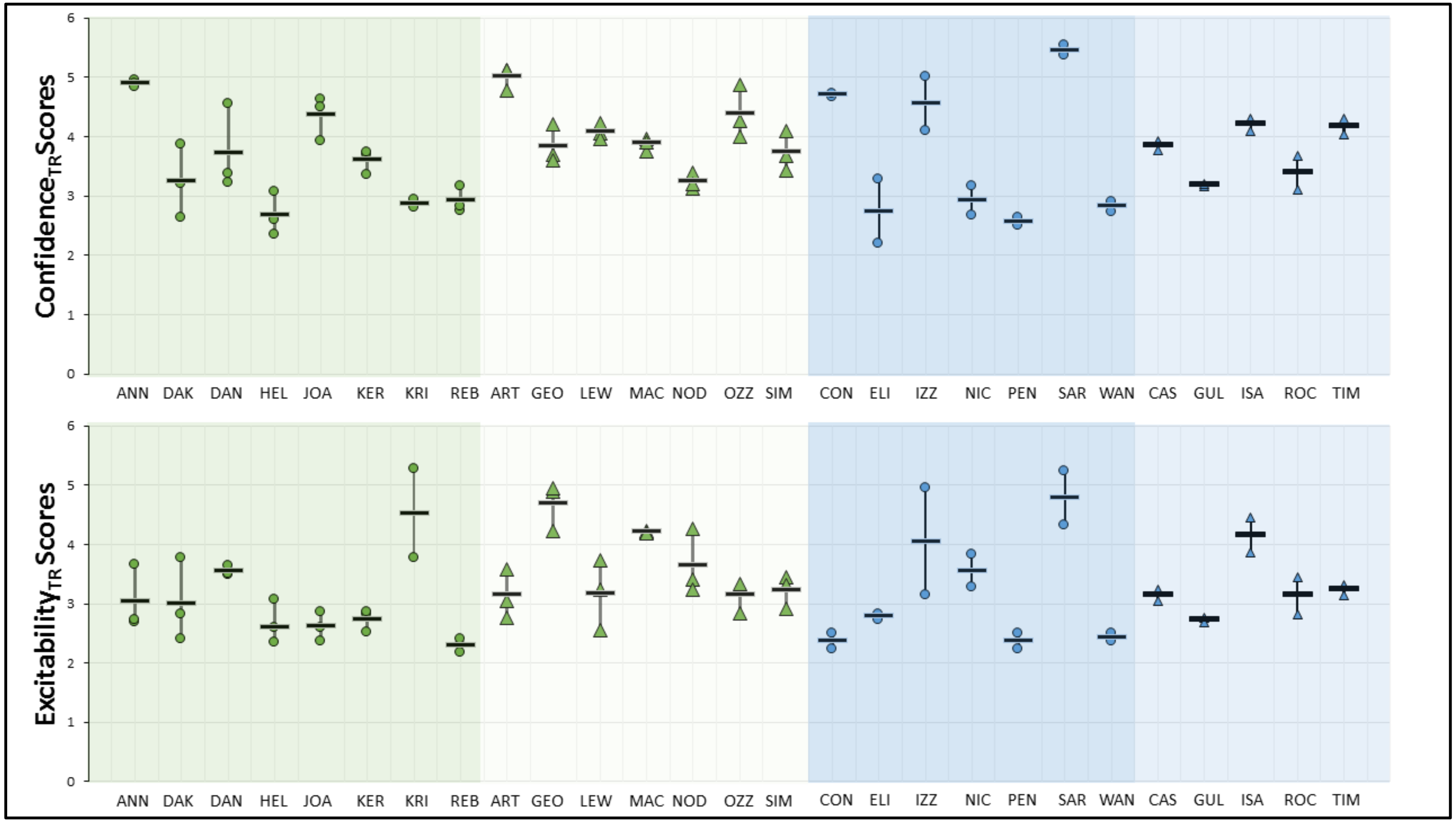


Figure 3.7: Confidence$_{TR}$ and Excitability$_{TR}$ scores for subjects (n=69). Each plot represents an individual score by a subject, the black bars represent mean score for a subject. Subjects are ordered by group (Green and Blue Group coloured green and blue respectively) and sex (females represented by ●; males represented by▲).

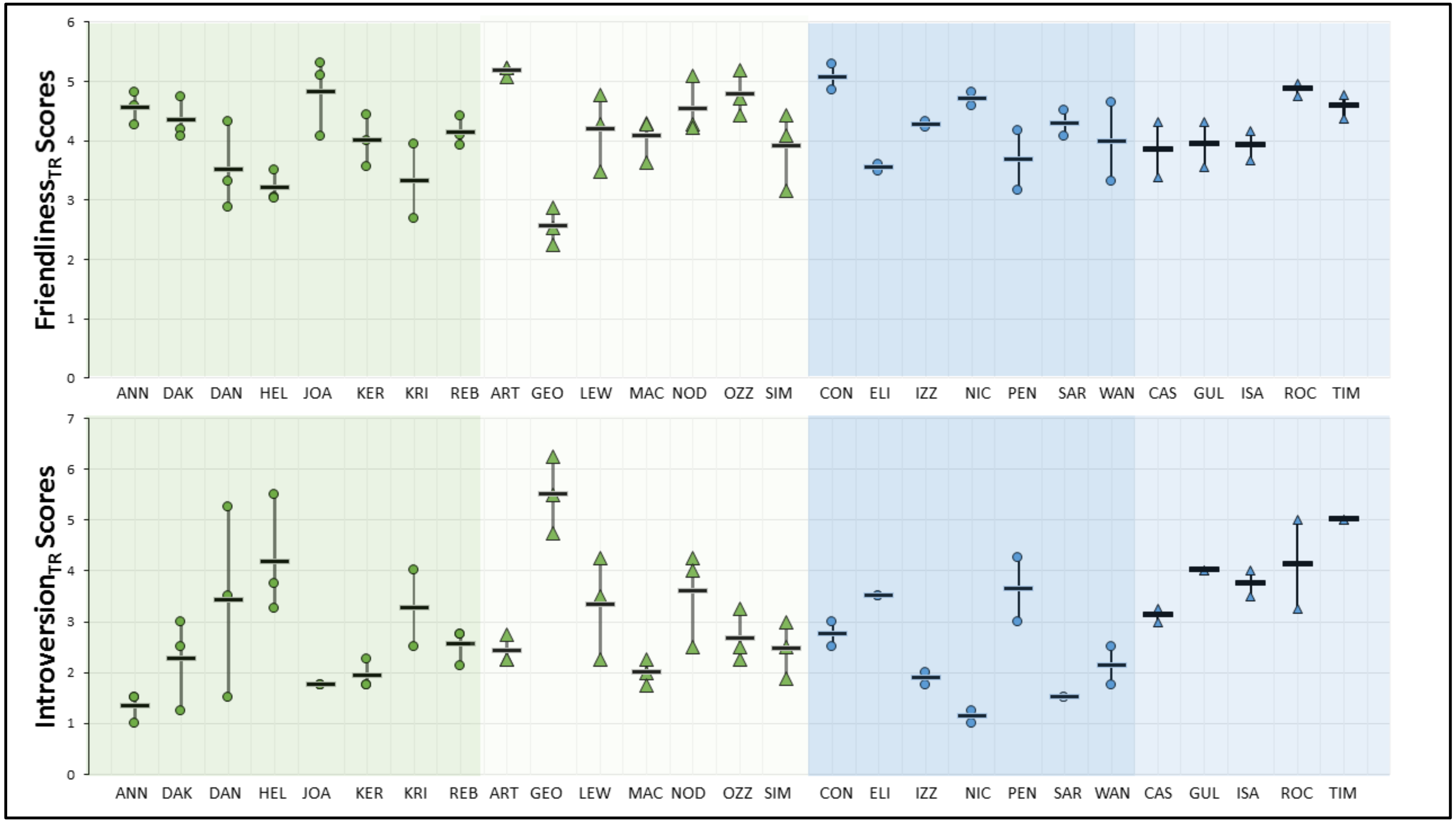


Figure 3.8: Friendliness$_{TR}$ and Introversion$_{TR}$ scores for subjects (n=69). Each plot represents an individual score by a subject, the black bars represent mean score for a subject. Subjects are ordered by group (Green and Blue Group coloured green and blue respectively) and sex (females represented by ●; males represented by ▲).

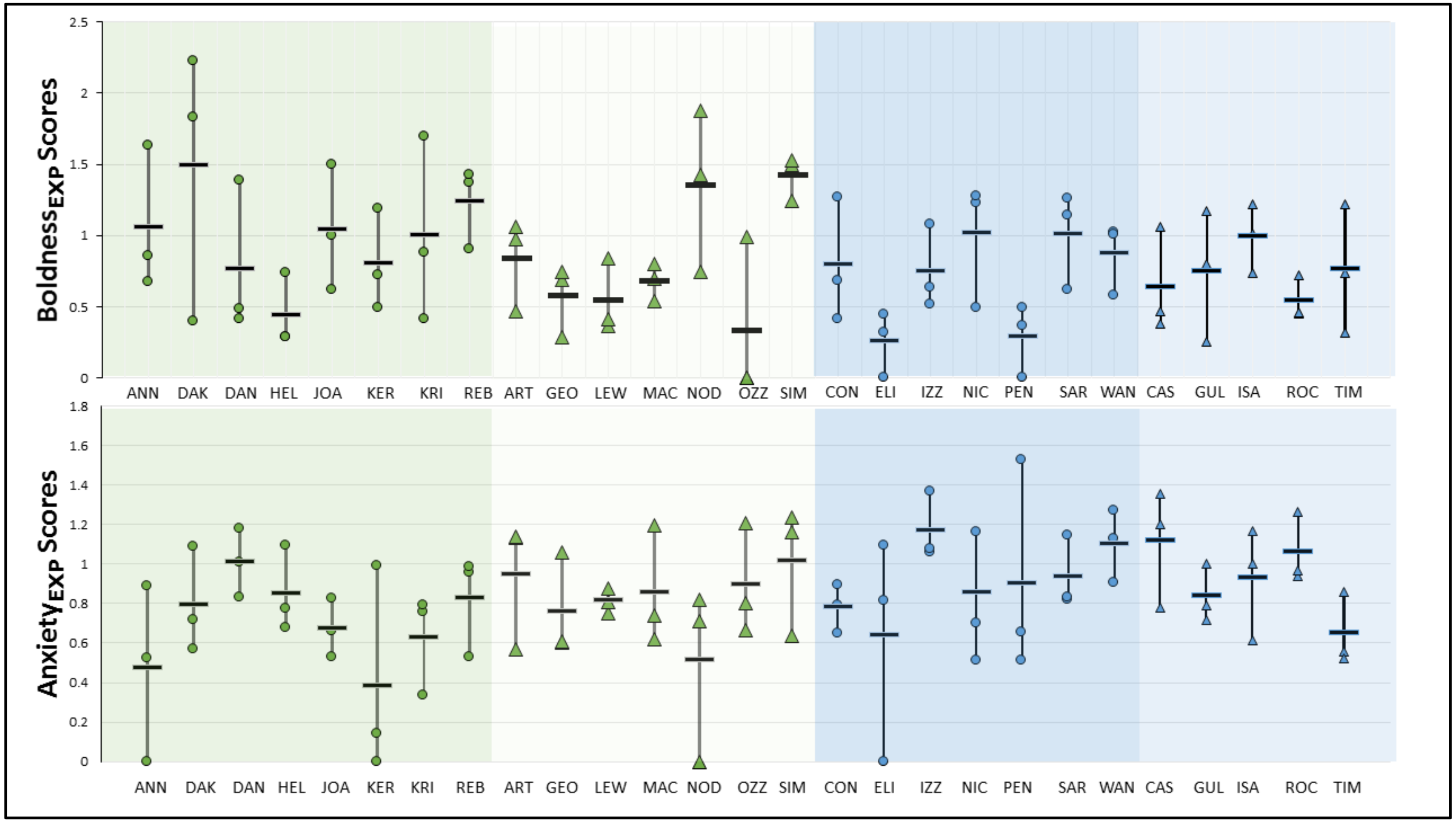


Figure 3.9: Boldness$_{\text{EXP}}$ and Anxiety$_{\text{EXP}}$ scores for subjects (n=81). Each plot represents an individual score by a subject, the black bars represent mean score for a subject. Subjects are ordered by group (Green and Blue Group coloured green and blue respectively) and sex (females represented by ●; males represented by▲).

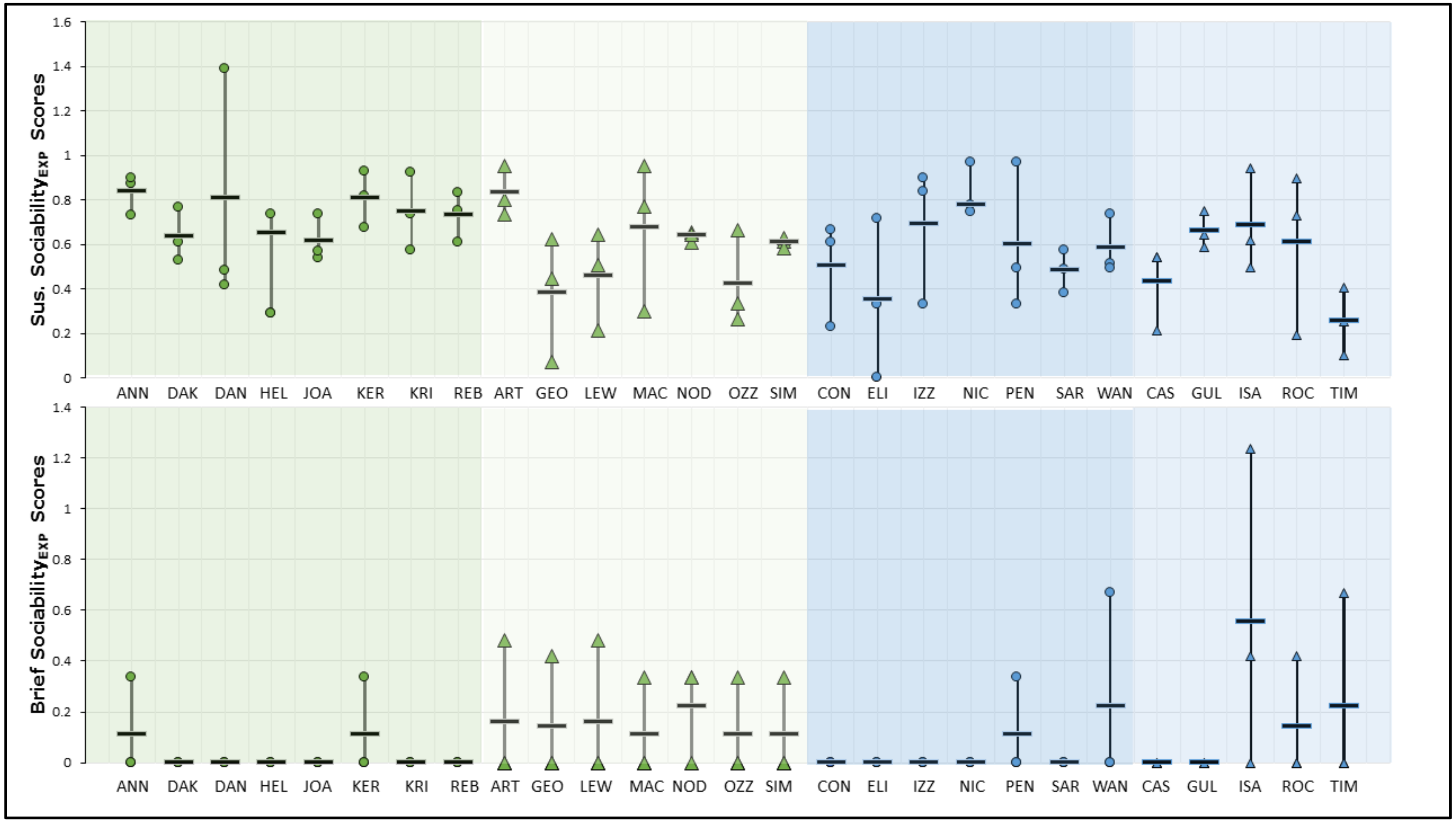


Figure 3.10: Sustained Sociability$_{EXP}$ and Brief Sociability$_{EXP}$ scores for subjects (n=81). Each plot represents an individual score by a subject, the black bars represent mean score for a subject. Subjects are ordered by group (Green and Blue Group coloured green and blue respectively) and sex (females represented by ●; males represented by▲).

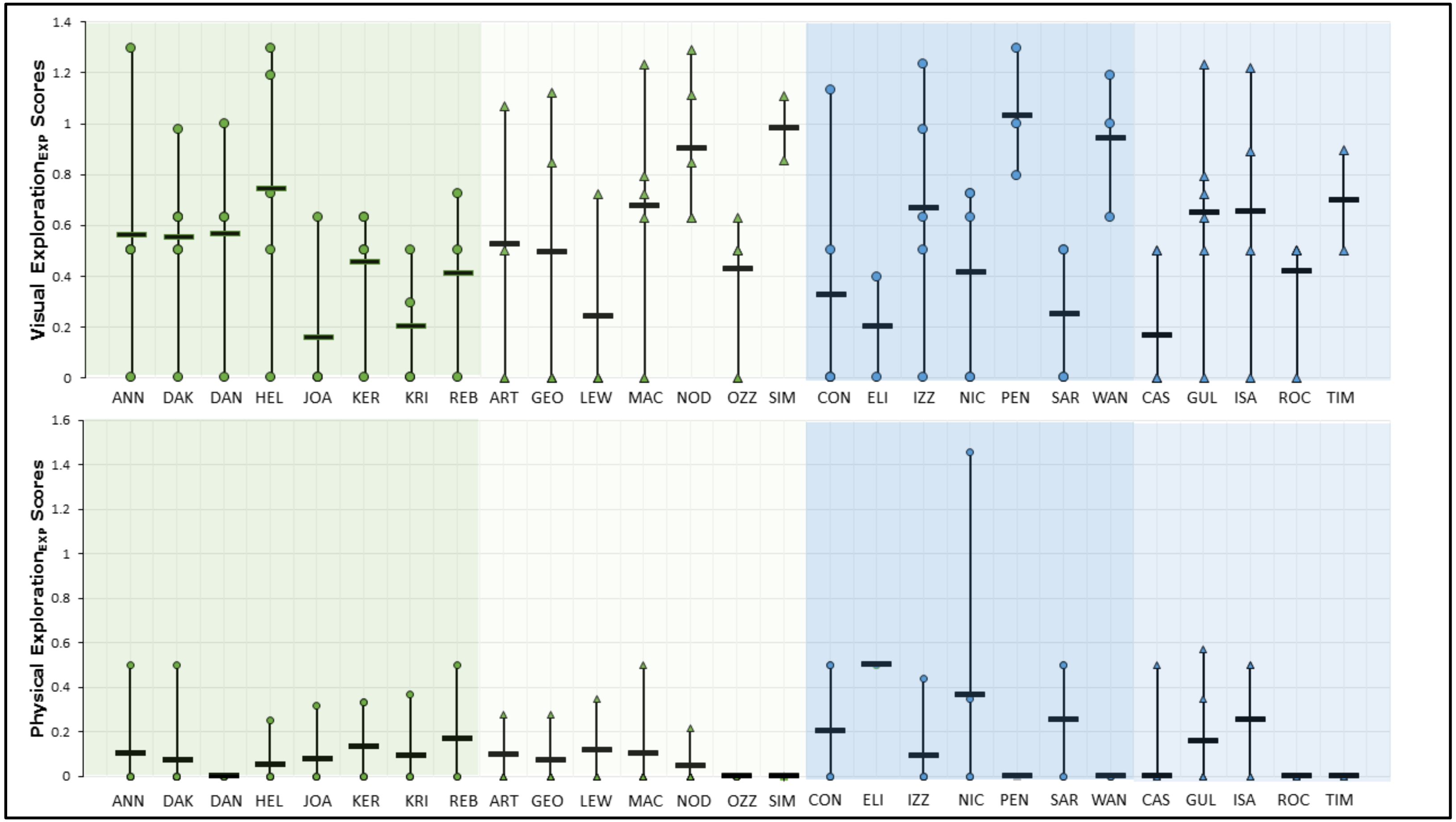


Figure 3.11: Visual Exploration$_{EXP}$ and Physical Exploration$_{EXP}$ scores for subjects (n=113). Each plot represents an individual score by a subject, the black bars represent mean score for a subject. Subjects are ordered by group (Green and Blue Group coloured green and blue respectively) and sex (females represented by ●; males represented by▲).

3.3.3 Relation of Behavioural Variables to Trait Rating- and Experimental Assay-Derived Personality Constructs

Mean personality scores per subject for both trait rating- and experimental assay-derived constructs were found to correlate with mean behavioural variable values per subject, providing evidence these constructs correlate with appropriate behaviours observed in a “real-world” setting”.

Personality constructs derived from trait rating correlated with 28 of 31 behavioural variables (mean behavioural variables per construct = 7.00[±4.58]; table 3.19); six of the behavioural variables correlated with more than one personality construct. Significant correlations revealed relationships with behavioural variables consistent with the meanings of the personality constructs. Introversion$_{TR}$ had three notable significant correlations where the meaning of the personality construct was inconsistent with its correlated behavioural variable. Introversion$_{TR}$ had significant positive correlations with grooming evenness (a measure of the distribution of grooming amongst available grooming partners), embraces and genital touches (both affiliative behaviours).

Personality constructs derived from playback experimental assays correlated with 23 of 31 behavioural variables (mean behavioural variables per construct = 5.75[±4.58]; table 3.20); five of the behavioural variables correlated with more than one personality construct. Correlations were generally consistent with the meanings of the personality constructs, e.g. Sustained Sociability$_{EXP}$ was positively correlated with several measures of allogrooming and Brief Sociability$_{EXP}$ was positively correlated with several brief affiliative interactions. Boldness$_{EXP}$ was positively correlated with several prosocial measures (allogrooming, numbers of neighbours within 0-1m), Anxiety$_{EXP}$ was positively correlated with being aggressive (both contact and non-contact), as well as the frequency of sandwiching, a social bonding mechanism in Barbary macaques.

Personality constructs derived from novel object experimental assays correlated with 3 of 31 behavioural variables (mean behavioural variables per construct = 1.50[$\pm$0.50]; table 3.21). Visual Exploration$_{EXP}$ positively correlated with self-scratch frequency; Physical Exploration$_{EXP}$ positively correlated with proportion of scans observed at the centre of the group, and negatively with proportion of scans spent at the edge of the group.

Table 3.19: Percentage bend correlations between subject means for behavioural variables collected for behavioural coding and trait rating-derived personality constructs (n = 27). Significant correlations are in bold (p<0.05).

Behaviour variable	**Confidence$_{TR}$**	**Excitability$_{TR}$**	**Friendliness$_{TR}$**	**Introversion$_{TR}$**
Activity	-0.11	-0.13	-0.09	-0.34
Submissions	0.01	-0.01	-0.15	-0.17
Retreats	-0.33	-0.34	-0.02	-0.00
Supplants	0.26	**0.39**	0.07	-0.10
Self-groom	-0.18	-0.05	-0.06	-0.23
Self-scratch	-0.17	0.21	-0.25	**0.48**
Body shake	0.06	-0.31	0.19	-0.01
Yawn	0.14	0.25	0.10	**0.45**
Tree shake	0.09	0.34	-0.14	**0.43**
Mounting	0.16	**0.38**	0.04	0.35
Allogrooming	-0.23	-0.11	-0.02	**-0.51**
Grooming density	-0.25	-0.08	-0.11	**-0.47**
Grooming diversity	-0.27	-0.05	-0.25	-0.24
Grooming evenness	-0.08	-0.20	-0.07	**0.41**
Vigilance	-0.31	0.05	-0.34	-0.16
Contact aggression	0.29	**0.40**	0.07	-0.14
Non-contact aggression	**0.40**	**0.56**	-0.03	-0.06
Open mouth	0.21	0.24	-0.07	0.19
Bare teeth	**0.39**	0.11	0.12	**0.38**
Teeth chatter	0.15	0.16	-0.22	**0.43**
Lip smack	0.01	**0.37**	0.04	**0.41**
Embrace	0.25	0.21	0.31	**0.40**
Genital touch	-0.05	**0.48**	0.05	**0.41**
Sandwich	0.23	**0.42**	0.07	0.07
Gaze	0.02	0.10	-0.22	-0.13
Edge of group	-0.19	-0.25	**-0.37**	**0.41**
Centre of group	0.19	0.25	**0.37**	**-0.41**
Neighbours within 0-1m	-0.04	-0.05	0.06	**-0.41**
Neighbours within 1-5m	0.26	0.22	**0.46**	-0.17
Neighbours within 5-10m	0.18	0.26	**0.37**	-0.29
Approaches	0.20	**0.49**	0.25	0.06

Table 3.20: Percentage bend correlations between subject means for behavioural variables collected for behavioural coding and playback experimental assay-derived personality constructs (n = 27). Significant correlations are in bold (p<0.05)

Behaviour variable	**Boldness$_{EXP}$**	**Sustained Sociability $_{EXP}$**	**Brief Sociability $_{EXP}$**	**Anxiety$_{EXP}$**
Activity	0.28	**0.55**	-0.20	-0.17
Submissions	0.15	0.32	-0.03	-0.27
Retreats	-0.04	-0.10	-0.31	-0.05
Supplants	0.19	-0.06	0.14	0.10
Self-groom	0.06	-0.06	-0.11	0.06
Self-scratch	-0.32	**-0.47**	**0.39**	0.23
Body shake	-0.19	-0.06	-0.33	-0.29
Yawn	-0.14	-0.22	**0.53**	0.20
Tree shake	0.00	-0.12	**0.46**	0.22
Mounting	-0.03	-0.29	**0.55**	0.19
Allogrooming	**0.47**	**0.57**	-0.32	0.05
Grooming density	**0.43**	**0.58**	**-0.48**	0.05
Grooming diversity	0.36	**0.44**	-0.23	-0.11
Grooming evenness	**-0.39**	**-0.58**	0.09	0.22
Vigilance	0.29	0.36	-0.18	-0.08
Contact aggression	0.22	0.27	0.09	**0.39**
Non-contact aggression	0.09	-0.27	-0.01	**0.42**
Open mouth	0.01	0.09	0.17	0.25
Bare teeth	-0.34	-0.25	0.27	0.24
Teeth chatter	-0.23	0.09	**0.40**	0.26
Lip smack	0.15	-0.15	0.26	-0.09
Embrace	-0.09	-0.15	**0.45**	0.16
Genital touch	0.04	0.15	0.11	0.12
Sandwich	0.25	-0.05	**0.37**	**0.40**
Gaze	0.11	0.36	-0.21	-0.31
Edge of group	-0.26	-0.30	0.25	-0.12
Centre of group	0.26	0.30	-0.25	0.12
Neighbours within 0-1m	**0.45**	0.24	-0.02	0.08
Neighbours within 1-5m	0.29	0.25	0.25	0.18
Neighbours within 5-10m	0.20	**0.40**	-0.14	0.21
Approaches	0.03	-0.13	0.01	0.33

Table 3.21: Percentage bend correlations between subject means for behavioural variables collected for behavioural coding and novel object experimental assay-derived personality constructs (n = 27). Significant correlations are in bold (p<0.05).

Behaviour variable	Visual Exploration$_{EXP}$	Physical Exploration$_{EXP}$
Activity	0.13	-0.31
Submissions	0.02	0.08
Retreats	-0.05	0.12
Supplants	-0.05	0.02
Self-groom	0.24	0.21
Self-scratch	**0.44**	0.25
Body shake	-0.08	0.16
Yawn	0.27	-0.15
Tree shake	0.24	-0.05
Mounting	0.28	-0.10
Allogrooming	0.05	0.08
Grooming density	0.03	-0.00
Grooming diversity	-0.01	-0.12
Grooming evenness	0.11	0.03
Vigilance	0.01	-0.18
Contact aggression	-0.02	0.26
Non-contact aggression	-0.05	0.19
Open mouth	0.11	0.14
Bare teeth	0.00	-0.02
Teeth chatter	0.28	-0.22
Lip smack	0.01	-0.12
Embrace	0.01	0.07
Genital touch	0.07	0.05
Sandwich	0.33	0.02
Gaze	0.00	-0.22
Edge of group	0.25	**-0.42**
Centre of group	-0.25	**0.42**
Neighbours within 0-1m	0.07	0.28
Neighbours within 1-5m	0.06	0.20
Neighbours within 5-10m	-0.16	0.17
Approaches	-0.18	0.33

3.3.4 Convergent and Discriminant Validity of Personality Constructs

Evidence for convergent validity was demonstrated by several correlations between behavioural coding- and trait rating-derived personality constructs (table 3.22). Excluding Confidence$_{\mathrm{TR}}$, each of the other trait rating-derived constructs correlated with at least one behavioural coding-derived construct. Figure 3.12 illustrates these correlations.

Evidence for discriminant validity was demonstrated by the limited correlations between experimental assay-derived constructs. Excluding Brief Sociability$_{\mathrm{EXP}}$, no other correlations were found between playback and novel object-derived constructs. Brief Sociability$_{\mathrm{EXP}}$ correlated positively with Visual Exploration$_{\mathrm{EXP}}$ and negatively with Physical Exploration$_{\mathrm{EXP}}$.

3.3.5 Barbary Macaque Personality Structure

Table 3.23 highlights the personality constructs to be considered representative of Barbary macaque personality based on three criteria (see section 3.2.5). Figure 3.12 visualises retained personality constructs and overall structure of Barbary macaque personality. Nine constructs were retained. Neuroticism$_{\mathrm{BC}}$, Anxiety$_{\mathrm{EXP}}$, Sustained Sociability$_{\mathrm{EXP}}$, Brief Sociability$_{\mathrm{EXP}}$ and Physical Exploration$_{\mathrm{EXP}}$ were not retained as subjects did not demonstrate intra-individual consistency for these constructs.

Table 3.22: Percentage bend correlations between subject mean scores for all personality constructs (n = 27). Significant correlations are in bold (p<0.05).

	Excitability$_{BC}$	**Sociability$_{BC}$**	**Tactility$_{BC}$**	**Neuroticism$_{BC}$**
Confidence$_{TR}$	0.28	0.21	-0.22	-0.29
Excitability$_{TR}$	**0.38**	0.26	-0.10	**-0.38**
Friendliness$_{TR}$	0.10	**0.39**	-0.05	0.03
Introversion$_{TR}$	-0.33	-0.35	**-0.55**	0.00
Boldness$_{EXP}$	0.00	0.22	**0.49**	-0.09
Sustained Sociability$_{EXP}$	-0.12	0.32	**0.54**	-0.11
Brief Sociability$_{EXP}$	**0.47**	-0.20	**-0.40**	-0.32
Anxiety$_{EXP}$	0.30	0.15	0.12	-0.10
Visual Exploration$_{EXP}$	0.24	-0.23	0.05	-0.04
Physical Exploration$_{EXP}$	-0.01	0.32	0.11	0.11

	Confidence$_{TR}$	**Excitability$_{TR}$**	**Friendliness$_{TR}$**	**Introversion$_{TR}$**
Boldness$_{EXP}$	0.07	0.14	0.25	**-0.45**
Sustained Sociability$_{EXP}$	-0.11	0.05	0.02	-0.34
Brief Sociability$_{EXP}$	0.17	0.12	0.18	0.23
Anxiety$_{EXP}$	0.07	0.09	-0.04	-0.03
Visual Exploration$_{EXP}$	-0.20	-0.02	-0.14	0.17
Physical Exploration$_{EXP}$	0.14	0.02	0.03	-0.29

	Boldness$_{EXP}$	**Sustained Sociability$_{EXP}$**	**Brief Sociability$_{EXP}$**	**Anxiety$_{EXP}$**
Visual Exploration$_{EXP}$	0.11	0.23	**0.46**	0.23
Physical Exploration$_{EXP}$	0.14	0.12	**-0.38**	-0.19

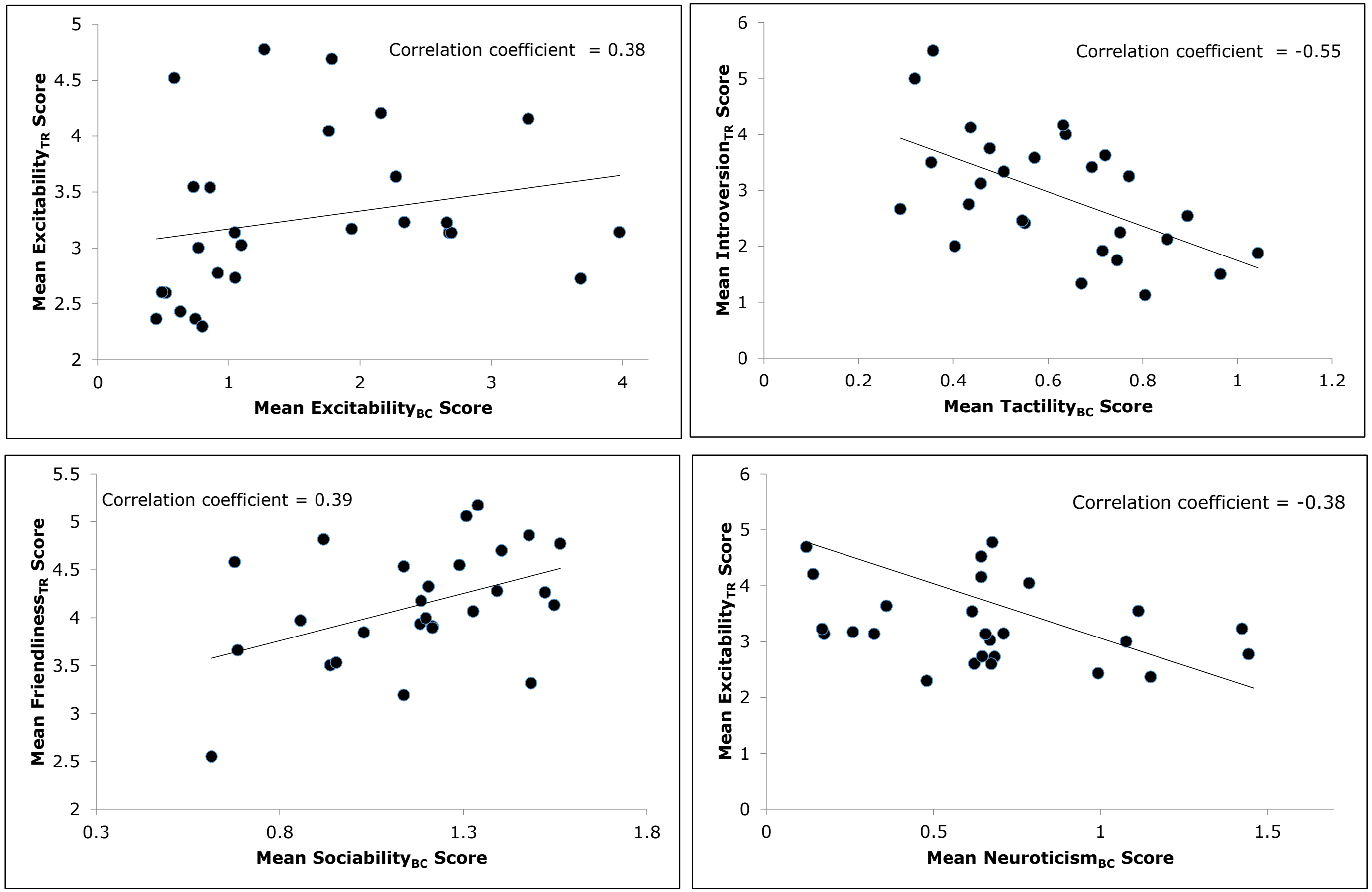


Figure 3.12. Significant correlations between behavioural coding- and trait rating-derived personality constructs. Plots represent mean score for a subject for a particular personality construct (n=27 for each scatterplot), regression lines represent the correlation between the personality scores..

Table 3.23: Adherence of all derived constructs to three criteria for retention for further analyses. Constructs which are to be retained are in bold, adherence to criteria is indicated by a (✓), non-adherence (X) and conditional adherences (*, **, *, ****, *****), with these conditions described below the table.**

Construct	C1: Inter-individual variation	C2: Intra-individual consistency	C3: Reflects natural behaviour	Retained
Excitability$_{BC}$	✓	✓	NA	✓
Sociability$_{BC}$	✓	✓	NA	✓
Tactility$_{BC}$	✓	✓	NA	✓
Neuroticism$_{BC}$	✓	X	NA	X
Confidence$_{TR}$	✓	✓	✓	✓
Excitability$_{TR}$	✓	✓	✓	✓
Friendliness$_{TR}$	✓	✓	✓	✓
Introversion$_{TR}$	✓	✓	✓	✓
Boldness$_{EXP}$	✓	✓	*	✓
Sustained Sociability$_{EXP}$	X	X	✓	X
Brief Sociability$_{EXP}$	X	X	✓	X
Anxiety$_{EXP}$	X	X	**	X
Visual Exploration$_{EXP}$	✓	X***	****	✓
Physical Exploration$_{EXP}$	X	✓	*****	X

* Correlated with prosocial behaviours.
** Correlated with aggressive behaviours.
*** Measure of intra-individual consistency approached significance ($R_A = 0.09$; $p = 0.08$).
**** Correlated with self-scratching.
***** Correlated with time spent in the centre of the group.

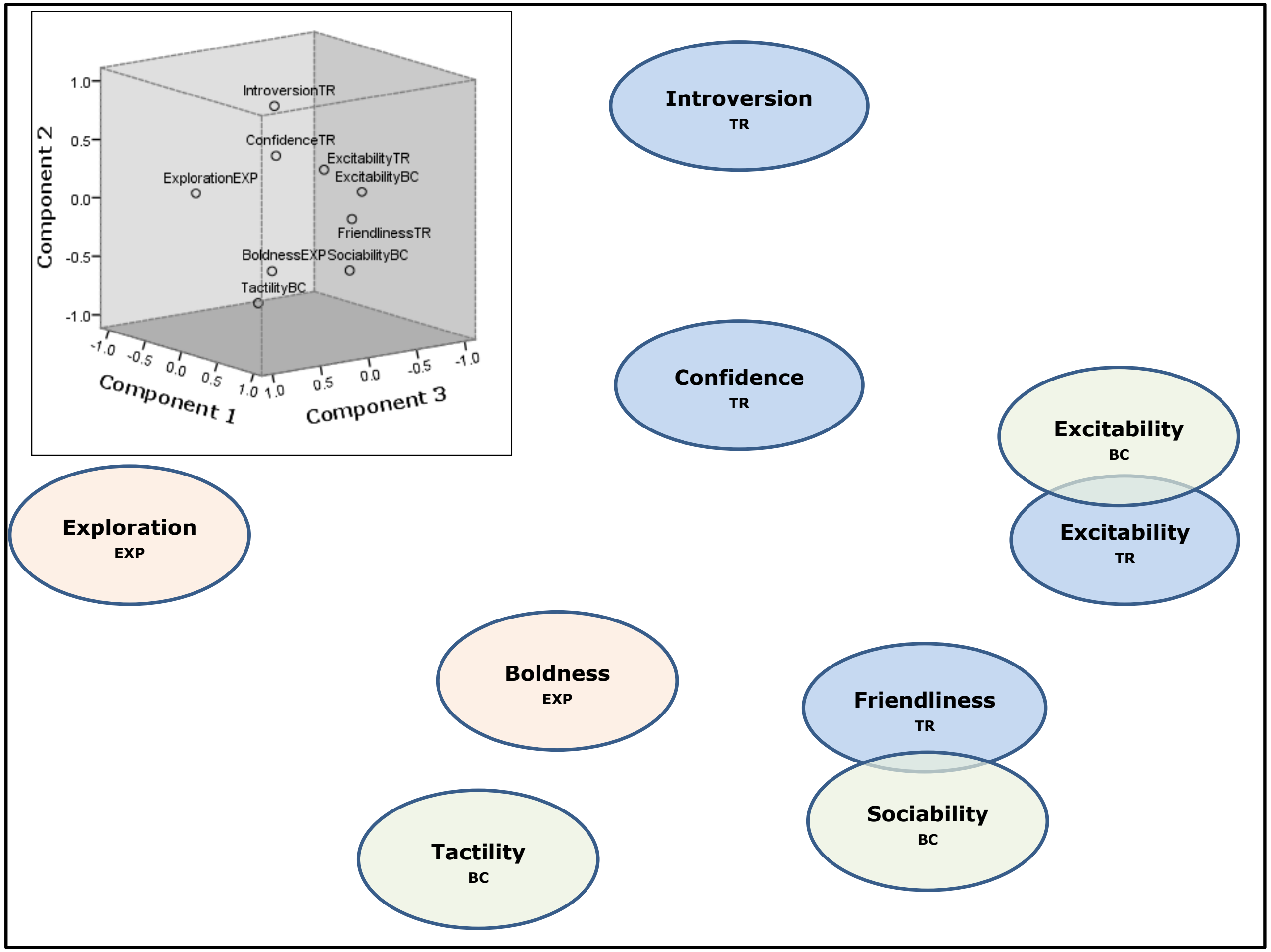


Figure 3.13: Diagram of Barbary macaque personality structure: the diagram is a simplified representation of a covariance component plot of mean scores for retained personality constructs (inset on figure). Colours of a construct reflect the method by which it was derived. Overlapping constructs had positive correlations for mean subject scores.

3.4 Discussion

3.4.1 Personality Constructs of Wild Barbary Macaques

This study identified nine personality constructs in wild Barbary macaques, some of which bear similarity to those found in previous Barbary macaque research (Konečá et al, 2012), as well as personality studies in other macaque species (Weiss et al 2011; Neumann et al, 2013; Adams et al, 2015) and primates more generally (Freeman & Gosling, 2010; Freeman, 2011). A number of correlations existed between constructs derived using different methodologies, demonstrating "convergent validity" in some circumstances, outlined in detail below. Furthermore, several constructs quantified using experimental- and questionnaire-based methods were found to correlate with behaviours observed in a non-experimental, natural setting. These findings are used below to describe Barbary macaque personality structure and relate to that of other primates.

"Excitability" was identified using both factor-based methodological approaches, and a significant positive correlation was seen between the mean subject expression of Excitability$_{BC}$ and Excitability$_{TR}$. "Excitability" has previously been identified in Barbary macaques using trait rating methods, where it was found to bear similarity with the construct "Openness" (Konečá et al, 2012; Adams et al, 2015), a personality construct which has been proposed to be a general feature of primate personality (Freeman & Gosling, 2010). Based on the similarity in structure and convergent validity of Excitability$_{BC}$ and Excitability$_{TR}$, the two structures are likely measuring the same broad construct present in Barbary macaques, which hereafter will be referred to as Excitability.

In other species, "Openness" and its analogues refer to curiosity, interest in exploration and play, as well as low impulse control (Gosling & John, 1999). Excitability found here largely contains elements related to low impulse control, with little evidence of curiosity, neophilia or exploration. During analysis of the questionnaire trait rating data, seven items from the questionnaire were unreliably rated. These unreliable items included "explorative", "curious", "opportunistic" and "inventive". However, previous work using this methodology to assay Barbary macaque personality found traits such as "inquisitive" (Adams et al, 2015) or "explorative" (Konečá et al, 2012) within the "Openness/Excitability" dimension. This variation between populations may be due to environment and the opportunities presented to demonstrate explorative or inquisitive behaviour to raters.

"Openness" or evidence of "curious" personality-phenotypes have twice been found to be absent in crested macaques (Neumann et al, 2013; Adams et al, 2015), and in this study, Barbary macaques also seem to have incurious personalities. It has been argued that despotic societies with low tolerance may favour selection for personality traits where curiosity and ingenuity can overcome intense inter-individual competition, whereas egalitarian social systems may favour selection for more complex prosocial personality phenotypes (Weiss et al, 2011). Thierry (2007) graded macaque species based on the degree of tolerance to conspecifics observed within their social groups; the lower the grade, the lower the tolerance on a scale of 1-4. Barbary macaques were considered grade 3, crested macaques grade 4. Further examination of differences in neophilia and exploration between species, or between populations given the variation observed in Barbary macaques, may be informative of the interplay between environment, social structure and personality.

Expressions of Sociability_{BC} and Friendliness_{TR} were positively correlated in this study. "Friendliness" has been proposed as a ubiquitous personality construct among macaques, regardless of the social style of the species and has previously been found in Barbary, rhesus, Assamese (*M. assamensis*), Tonkean (*M. tonkeana*), and Japanese macaques (*M. fuscata*; Konečá et al, 2012; Neumann et al, 2013; Adams et al, 2015). Based on the similarity in structure and evidence of convergent validity, as was the case for $\text{Excitability}_{\text{BC}}$ and $\text{Excitability}_{\text{TR}}$, it is proposed that $\text{Sociability}_{\text{BC}}$ and $\text{Friendliness}_{\text{TR}}$ are measuring the same broad construct that hereafter will be referred to as Sociability.

In humans and some great ape species, social personality has generally been split across two dimensions, "Extraversion" and "Agreeableness" (McCrae & John, 1992; Gold & Maple, 1994; King & Figuerdo, 1997; Weiss et al 2011). It has been argued that the "Friendliness" dimension of macaques is a "blended" dimension, incorporating elements of "Extraversion" and "Agreeableness" which have since become decoupled in the course of social evolution (Adams et al, 2015). In this study, behavioural coding identified a second personality construct strongly linked with sociality, $\text{Tactility}_{\text{BC}}$, which constituted variables related to rates of self- and allogrooming. Expression of $\text{Tactility}_{\text{BC}}$ was uncorrelated with Sociability and negatively correlated with $\text{Introversion}_{\text{TR}}$, a construct characterised by low sociability and solitary behaviour. $\text{Tactility}_{\text{BC}}$ and Sociability, therefore, appear to be two independent social personality constructs. Tonkean and crested macaques were previously the only macaque species studied to date to mirror hominins in the split of social personality across two constructs (Neumann et al, 2013; Adams et al, 2015). Species social structure may explain this relative diversity of social personality. It has also been suggested that the "Connectedness" dimension found in crested macaques (identified alongside the more general social dimension "Sociability"), which refers to the diversity of social partners, may have adaptive fitness benefits for a species where coalitions are an important factor in agonistic interactions (Neumann et al, 2013). In Barbary macaques, subjects form complex coalitions and relationships which are reinforced by a series of either brief (adult-infant-adult triadic embraces, or "sandwiches", and dyadic embraces) or sustained physical contact during grooming (Berghänel et al, 2011). Tolerant social structures may have allowed for the evolution of subtler and diverse social interactions in certain macaque species (Ciani et al, 2012), which are then reflected in personality constructs.

The inclusion of self-grooming within Tactility$_{BC}$, which is being described as a social personality construct, is interesting. In animal and primate studies, including those of Barbary macaques, self-grooming has been used as a measure of anxiety (Schino et al, 1996; Radford, 2012; Molesti & Majolo, 2013). In several Barbary macaque studies, allogrooming bouts can raise, rather than lower, anxiety levels (Molesti & Majolo, 2013; Semple et al, 2013) and the correlated traits constituting Tactility$_{BC}$ identified in the current project appear to replicate this relationship. Therefore, Tactility$_{BC}$ as a construct may reflect the consequences of being social for Barbary macaques.

"Boldness" is arguably the most well studied animal personality trait (Smith & Blumstein, 2008; Conrad et al, 2011; Carere & Maestripieri, 2013) and as described earlier in this chapter, is the subject of numerous terminological issues (Carter et al, 2012; Carter et al, 2013). Here, it was defined as a "positive and non-fearful" response to a risky situation (Réale et al, 2007), and was characterised by a series of affiliative and assertive behaviours when presented with a simulated inter-group encounter. Barbary macaque boldness may be an important element of social competence, reflecting an ability to face confrontation in a positive manner and build intra-group social bonds in the face of inter-group aggression. In other primate species, higher-ranking individuals participate more frequently in inter-group encounters than low-ranking individuals (Cooper et al, 2004). In white-faced capuchins, individuals which experienced more aggression from conspecifics were less likely to participate in group defence (Crofoot et al, 2011). Inter-group encounters remain relatively understudied in Barbary macaques, yet it is possible that higher-ranking or more socially connected individuals are likely to be the main participants in inter-group encounters and thus more likely to be stimulated by such a perceived threat. Relationships between personality constructs and social factors are explored in later chapters of this thesis.

Confidence$_{TR}$ was the only retained construct which did not correlate with any other identified construct. This construct constituted a very broad range of contributory variables (21 of the 51 items from the questionnaire were eventually included in this construct), including manipulative, selective and dominant. In previous primate personality research, constructs resembling Confidence$_{TR}$ found here have been called "Dominance", such as in chimpanzees (Koski, 2011; King & Figuerdo, 1997), Tonkean (Adams et al, 2015) Japanese (Adams et al, 2015) and rhesus macaques (Weiss et al, 2011). Analogues of Confidence$_{TR}$ appear to be a universal dimension among primates studied to date (Adams et al, 2015), which seems intuitive given its close association with dominance hierarchies and/or aggressive behaviours, which are found in most group-living mammals (Cummins, 1996).

Introversion$_{TR}$ has not previously been identified in Barbary macaques (Konečá et al, 2012; Adams et al, 2015). In other Barbary macaque personality studies, researchers identified "Irritability" in *wild* macaques (Adams et al, 2015), which can be considered an antisocial construct like Introversion$_{TR}$, and "Opportunism" in *semi-free ranging* macaques (Konečá et al, 2012). Wild

Barbary macaques may have the physical space to develop antisocial tendencies, whereas captive or semi-free ranging individuals may be forced into proximity with conspecifics, potentially inhibiting or promoting the expression of particular traits. In humans, personality structure varies between different sized societies and populations (Gurven et al, 2013). Ongoing comparative intra-specific research may further inform how personality develops or is able to be expressed in different environments.

In summary, this study found a personality structure for Barbary macaques which replicates and builds upon findings in previous studies in the species and other macaques. Based on the identified correlations, the nine retained constructs can be further reduced. Listed below are the constructs considered to be a complete representation of Barbary macaque personality and a summary of their relationship to known primate personality constructs from the literature:

- **Excitability** – analogous to primate "Openness".
- **Sociability** – analogous to macaque "Friendliness".
- **Confidence** (formerly $\text{Confidence}_{\text{TR}}$) – analogous to primate "Dominance".
- **Tactility** (formerly $\text{Tactility}_{\text{BC}}$) – construct so far unique to Barbary macaques; similar to "Connectedness" in crested macaques.
- **Introversion** (formerly $\text{Introversion}_{\text{TR}}$) – analogous to human "Introversion". Similar to "Irritability", previously found in another population of Barbary macaques.
- **Boldness** (formerly $\text{Boldness}_{\text{EXP}}$) – a trait found throughout many animal taxa (Koski, 2014).

- **Exploration** (formerly Visual Exploration$_{BM}$) – another trait common throughout animal taxa (Koski, 2014).

3.4.2 Methodological Considerations for Quantifying Personality in Wild Primates

Behavioural coding

The major advantage of behavioural coding of observation data is its relative objectivity (Freeman et al, 2011). Some subjectivity remains in the choice of behaviours to include in the ethogram and there are dangers of observer bias when collecting data (Traniello & Bakker, 2015). However, behavioural coding reduces subjectivity by taking a "bottom-up" approach and using the behaviour of the subjects without any *a priori* assumptions about personality structure (Seyfarth et al, 2012).

Behavioural coding has several significant disadvantages though. Principally, it is time consuming, requiring several hours of data collection across time and context to account for variation in behaviour (Freeman et al, 2011). While trait rating requires raters to have long-term familiarity with subjects, an individual researcher can draw on previous researcher's experiences and collect personality data in a relatively short time period. Time dependency is particularly problematic when studying wild animals, where climate, reproductive season, food availability and degrees of disturbance (either natural or anthropogenic) influence the frequencies of behaviours which can only be controlled by long-term data collection (Réale et al, 2007). In this study, consistency in the expression of behavioural coding-derived constructs was significant ($p<0.05$), with the exception of Neuroticism$_{BC}$. Visual inspection of the data suggests that this construct may be highly affected by seasonality, with generally higher subject scores for the construct during mating season. Data collection was skewed in the present study, with more data collection occurring outside of the mating season than within (section 2.4.3). Personality is classically defined as inter-individual differences in consistent behaviour over time and context (Réale et al, 2007); however, recent refinement of personality definitions propose that individuals vary not only in their average behaviour but also in their degree of behavioural flexibility (Dingemanse & Wolf, 2010). A more balanced (in terms of season) and longer-term study design could allow fuller investigation of the degree to which individuals increase displaying “neurotic” behaviours during competitive reproductive seasons and whether this is consistent.

It is essential that researchers carefully consider the time frame of their study with reference to the environment of their chosen subjects. For example, if studying arboreal primates where visibility requires behaviour to be collected using short focal or instantaneous sampling methods (Kays & Allison, 2001), observers risk missing infrequent yet key personality-related behaviours (Martin et al, 1993; Freeman et al, 2011). Many primate species exhibit remarkable adaptation to highly variable climatic environments. For example, both Barbary and Japanese macaques live in climatic zones featuring extreme cold in winter and high temperatures in summer (Cozzolino et al, 1992; Majolo et al, 2013), placing constraints on the variety of behaviours that can be expressed. In Barbary macaques, play behaviours are rarely seen during winter where behaviour is foraging-focused, yet come spring, play among adults, juveniles and infants is seen frequently throughout the day (personal observation, 2015). Similarly, a number of primate species exhibit breeding seasonality (Paul, 1997). Some species have unique behavioural repertoires seen only during mating seasons. For example, female tufted capuchins solicit males using complex vocal and behavioural sequences to lure males away from the social group for copulations (Carosi & Visalberghi, 2002). Furthermore, inter-sex competition during mating season is likely to influence the rates of various personality-associated behaviours such as aggression, cooperation and reconciliation (Cavigelli & Perreira, 2000; Young et al, 2014b).

Trait rating

The immediate issue raised with the trait rating methodology is its inherent anthropomorphism (Gosling & John, 1999). Researchers continue to develop their own species-specific questionnaires and items (Gosling, 1998; Freeman et al, 2011). However, it remains that most traits being described and quantified in animals originate from corresponding traits in humans (Weiss et al, 2011). This becomes further problematic in comparative studies and can lead to false assumptions that a trait is present in one species, as well as in humans, simply because we have attributed the trait to the animal species (Kennedy, 1992). This disadvantage can be overcome through functional validation, whereby dimensions of personality generated by trait rating are compared to the actual behavioural repertoire of the species (Koski, 2011). Within primatology, this has generally produced positive correlations (Capitanio, 1999; Pederson et al, 2005; Vazire et al, 2007; Konečá et al, 2008; Uher & Asendorpf, 2008; Carter et al, 2012). In the study presented here, convergent validity was observed between several constructs generated by behavioural coding and trait rating. Furthermore, positive and negative correlations were observed between $\text{Introversion}_{\text{TR}}$ scores and rates of self-scratching and allogrooming respectively. This suggests that trait-rating constructs in this study do reflect some elements of the Barbary macaque behavioural repertoire.

When studying wild primates, researchers may be working in remote regions and a major issue with trait rating is likely to be finding participants suitably familiar with the subjects to be capable of reliably rating personality (Koski, 2011). Participants need to be capable of identifying individual primates and retaining a mental impression of the subject's characteristics in order to complete the questionnaires (Gosling & Vazire, 2002; Uher, 2008). For example, in the study presented here, for two of the seasons, only two raters were available, a low sample size for measuring inter-rater reliability (Biro & Stamps, 2015). Researchers in remote areas often have nothing more to discuss during free time than their primate subjects, which may create an unconscious bias and false reliability. Alternatively, with a limited number of raters, individual conceptions of traits may lead to discordance in ratings. For example, one person's notion of "friendly" or "sociable" may differ greatly from another's (Freeman et al, 2011). This may become particularly apparent when the raters come from different cultures or societies, which may be the case when recruiting a mix of foreign researchers and local field assistants as raters.

Experimental Assays

Experimental assays of personality in primates in laboratory or captive settings have a long and ongoing history (Hebb, 1949; Gold & Maple, 1994; Fairbanks et al, 2001; Sussman et al, 2013; Baker et al, 2015), and more recently there has been an effort to perform similar experiments in wild primates (Carter et al, 2012, 2014; Neumann et al, 2013). Performing experiments in the field creates numerous logistical difficulties. An obvious constraint is time. In the laboratory or captivity, control over the environment means that experiments can be conducted according to the schedule of the researcher. In the wild, climate, levels of disturbance, difficulty finding and isolating subjects, as well issues related to equipment can limit the number of experiments possible during a field season (Fischer et al, 2013). In any experimental design, researchers wish to avoid habituation of their subjects to stimuli. Depending on the habitat and the nature of the experiment, for example playback studies, it may not be possible to isolate individuals in the wild and thus conspecifics may be exposed to the stimulus even though they are not subjects (McGregor, 2000; Fischer et al, 2013).

In this study, to mitigate this issue, multiple subjects were studied per experiment to reduce the overall number of experiments conducted. In one weekly experiment, two to three subjects were assayed, which over the study period, enabled the project to perform at least three playback experiments per subject, and an average of four novel object experiments per subject. Although this allowed for rigorous testing of repeatable responses across these experiments (Bell, 2012), it did present issues in study design. For the playback experiments, it created an issue in terms of controlling the distance subjects were from the speaker at the time of the stimuli being played. Results showed that the position of individuals, that is, whether on the ground or not, had a significant effect on the expression of Boldness. If a subject was on the ground, it tended to express Boldness less, which is intuitive as animals in trees are potentially less exposed and less sensitive to danger and threats. For the novel object experiments, no control was placed over which subjects could enter proximity with the object in each experiment. Previous research has either used novel foods (Carter et al, 2012), objects baited with food (Carter et al, 2014) or directly placing novel objects in front of subjects (Arnaud et al, personal communication) in order to gain more control over when and where individuals approached an object. Depending on the chosen study species, these approaches may not be practical or ethical. Barbary macaques are an endangered species whose greatest threat comes from poaching and over-habituation to human presence and foods (Majolo et al, 2013). In this study, objects were suspended from trees in advance of the arrival of the subjects, with the aim of avoiding directly presenting the objects to the subjects. This also reduced control over the context for a subject when it encountered the novelty. Motivation to explore is highly context specific and can be strongly affected by social factors or current emotional state (Carter et al, 2013; Massen et al, 2013).

Experimental design, even in the controlled environment of a laboratory, is a fine art (Wiley, 2003). In personality research, the design of experiments requires a number of assumptions, for example, that the sound of a donkey is novel to crested macaques (Neumann et al, 2013), that changing the colour of a food item makes it novel to baboons (Carter et al, 2013) or that children's toys may be of interest to Barbary macaques in this study. For "Boldness" assays, researchers have often turned to predator models (Carter et al, 2012; Massen et al, 2013; Neumann et al, 2013; Koski & Burkardt, 2015). This approach reduces and addresses issues of ecological validity or non-interest from the subjects, although population differences have been observed in the degree to which they respond to predator models based on the relative threat those populations experience within their home range (Bshary, 2001).

In this study, results from the experiments suggest that there is merit in using experiments to illicit specific constructs that may independent of, or only partially related to broader constructs generated by behavioural coding and trait rating. Boldness was correlated with Tactility. However, both were constituted of different behaviours and Boldness was shown (via comparisons to control experiments) to be a specific response to a non-novel but threatening stimulus. In another study, Massen et al (2013) used an experimental approach which identified “tool-orientation” as a specific personality construct in chimpanzees. In both the case of Boldness$_{BM}$n Barbary macaques and tool-orientation in chimpanzees, these constructs would be too infrequently expressed to be quantified without experiment manipulation. Therefore, if the goal of the study is a “complete” characterisation of personality in a species, all three personality assessments may be necessary: behavioural coding and trait rating in combination for the course-scale constructs, complimented by experimental assays to determine fine-scale constructs that are ecologically valid to a species.

3.4.3 Which Methods should be used to Quantify Personality in Wild Primates?

No single method for assessing personality in wild primates is ideal, and the examples of convergent and divergent validity in this study make a compelling case that, where possible, all methods should be adopted to fully characterise the personality of chosen subject species. There are certainly no quick solutions to quantifying personality in wild primates and all researchers should seriously consider whether accurate personality assessment is achievable within the timeframe of their research. Behavioural coding requires many hours of data collection, trait rating necessitates long-term familiarity with the subjects and experimental approaches require several trials to have adequate sample sizes for repeatability, yet must be done over an appropriate timeframe to avoid habituation to chosen stimuli. That said, the main conclusion here is that behavioural coding and trait rating should be performed concurrently. The resulting personality constructs will provide a general and useful characterisation of personality in a wild primate. Experimental approaches are perhaps solely recommended when researchers have specific *a priori* hypotheses about the constructs that these methods can illicit.

4| Personality, Physiological Stress and Life History in Wild Barbary Macaques

Abstract

Personality is defined as inter-individual variation and intra-individual consistency in behaviour. The “state-dependent” hypothesis for the evolution and maintenance of personality posits that inter-individual variation in behavioural repertoires arises from inter-individual variation in state (i.e. body size, health, metabolism etc.) and that the relative stability of these states within an individual can be related to consistency of behaviour. Furthermore, the “pace-of-life” hypothesis suggests that inter-individual variation in state arises due to differences in life history stages. Endocrine functioning is a proposed personality-associated state: hormones can have multi-modal effects on behaviour, and thus personality, by determining the speed and strength of responses to the internal and external environment. The endocrine stress response is of particular interest in this respect as glucocorticoids are closely linked with an individual’s response to stressors, either homeostatic or extreme stressors, such as predators. In this study, the expression of personality in wild Barbary macaques is examined for associations with physiological stress levels, i.e. faecal glucocorticoid (fGC) concentrations and a measure of stress reactivity (coefficient of variation in fGC concentrations), as well as life history variables, i.e. sex, rank and age. Inter-individual variation and intra-individual consistency in fGC concentrations were demonstrated, supporting physiological stress as a factor which may be associated with personality expression. The expression of three personality constructs (Excitability, Tactility and Exploration) was related to stress physiology, and the relationships between personality and physiology

were sex- and in some cases, age-specific. These findings support both the “state-dependent” and “pace-of-life” hypotheses of personality.

4.1 Introduction

Personality is defined as intra-individual consistency and inter-individual variation in behavioural repertoires, while behavioural syndromes are classified as sets of two or more behavioural traits that are correlated over time and context (Réale et al, 2007; Carter et al, 2013). Such behavioural consistency may represent a constraint on behavioural flexibility, which seems potentially maladaptive (West-Eberhard, 1989; Wilson et al, 1994); therefore, within evolutionary ecology, theorists have sought adaptive models to explain personality’s widespread presence throughout the animal kingdom (Wolf & Weissing, 2010). The “state-dependent” hypothesis is an adaptive model for personality which posits that inter-individual variation in behavioural repertoires arises from inter-individual variation in “state” and that the relative stability of these states can be related to consistency of behaviour (Biro & Stamps, 2008). In terms of evolutionary ecology, states can be defined as features that affect the cost/benefit trade-offs in strategies related to increasing fitness (Houston & McNamara, 1999; Wolf & Weissing, 2010). Such features include individual characteristics such as morphology, health or physiology, or environmental factors such as type of habitat or social environment.

Variation in state within a population may arise as a consequence of variation in life history strategy between individuals (Réale et al, 2010). Studies in social primates have frequently linked certain personality traits to dominance, which is an important component of life history strategy in these species, influencing factors such as growth rate and competitiveness for resources

(Sprague et al, 1998; Johnson, 2003; Setchell et al, 2006). Behavioural repertoires are both a consequence of and a predictor of social status, which can make segregating dominance from personality difficult, particularly if hierarchies are stable (Favati et al, 2014). In Barbary macaques (*Macaca sylvanus*), chimpanzees (*Pan troglodytes*), white-faced capuchins (*Cebus capucinus*) and western mountain gorillas (*Gorilla berengei berengei*), the personality traits "Confidence", "Aggressive", "Assertiveness" and "Dominance" respectively were directly associated with dominance rank (Anestis, 2005; Konečná et al, 2012; Manson & Perry, 2013; Eckardt et al, 2015).

Within evolutionary ecology, there have also been recent efforts to understand the mechanistic links between life history and inter-individual variation in behaviour (Montiglio et al, 2015). Neuroendocrinology (the anatomical structures and processes which mediate the interaction between the nervous system and hormone expression) has been proposed as a personality-generating state, acting as a constraint on behavioural flexibility and dictating responses to social and environmental conditions (Sih et al, 2004; Carere et al, 2010; Wolf & Weissing, 2010; Duckworth & Sockman, 2012). The expression of hormones is a product of genetics and environmental situation (Ketterson & Nolan, 1999; Fairbanks et al, 2011), and hormones act on multiple target tissues with a broad influence on behaviour (Sih et al, 2004). In social primates, dominance rank, reproductive status and age also correlate with stress and cortisol reactivity (Ziegler et al, 1995; Sapolsky, 2005), suggesting a potential link between life history, state and personality.

Hormonal responses to stress are of particular interest; indeed Koolhaas et al (1999) conceptualised personality phenotypes as "coping styles" in response to environmental and social stressors. Individuals with relatively low stress activity or reactivity were described as "proactive" and would be expected to employ strategies to actively avoid stressors. Individuals with relatively high stress activity or reactivity were described as "reactive" and would be more likely to be more behaviourally flexible in their reponse to a stressor, either by utilising aggression or fleeing.

In vertebrates, the hypothalamus acts as the coordinating neuroendocrine centre, translating sensory information into hormonal responses via three main axes, namely the hypothalamic-pituitary-adrenal (HPA), hypothalamic-pituitary-thyroid and hypothalamic-pituitary-gonadal (HPG) axes (Muehlenbein, 2009). The major response to a stressor is activation of the HPA axis which stimulates the redirection of energy and behaviour via glucocorticoids (Sapolsky et al, 2000). Under the "Reactive Scope Model", the range in the expression of glucocorticoids in response to predictive and reactive stressors characterizes the normal reactive scope available to an individual and has been suggested to be an adaptive system to cope with varying environmental and social conditions (Romero et al, 2009). Extreme stressors may require a response outside of this normal reactive range and long-term extreme stress is associated with negative health consequences, such as muscle wastage, fat accumulation or reduced immunity (Sapolsky et al, 2000; Marsland et al, 2002). Therefore, physiological stress may have both a direct effect on behaviour, as it is associated with behavioural responses to stressors, such as motivation to avoid or confront a stressor, and an indirect effect on behaviour as it may affect behavioural repertoires via deleterious health.

Furthermore, stress reactivity has important associations with other hormonal processes which may influence the expression of behaviour. Testosterone is the primary androgen in vertebrates and concentrations fluctuate in response to a variety of social cues related to competition, dominance, social status and aggression (Sellers et al, 2007; Kornienko et al, 2014). The “dual-hormone” hypothesis states that cortisol, a glucocorticoid associated with stress response, and testosterone have a joint effect on motivation and behaviour (Zilioli et al, 2014). Cortisol and testosterone are connected via feedback loops, whereby high levels of cortisol can inhibit the HPG axis or high levels of testosterone can act upon the hypothalamus to inhibit cortisol release (Viau, 2002). Cortisol also appears to decrease circulating levels of thyroid hormones which may function to conserve energy and resources in an unpredictable environment, as these hormones also play a role in growth and metabolism (Engel & Schmale, 1972).

Evidently, physiological stress can have a multi-modal influence on the behavioural range of individuals. In order for stress to be an appropriate state to explain personality under the state-dependent hypothesis, as with personality, there should be evidence of inter-individual variation and intra-individual consistency in stress activity and reactivity within a species or population. Inter-individual variation in stress is well established in primates and has been linked to personality. In tufted capuchins (*Cebus apella*), ‘proactive’ individuals (aggressive, exploratory) have low HPA activation compared to ‘reactive’ (docile, non-exploratory) individuals (Byrne & Suomi, 2002). In rhesus macaques (*Macaca mulatta*), “excitable” individuals had low HPA activation compared to more inactive individuals (Capitiano et al, 2004). There is also some evidence that stress activity is a relatively stable state over time. In rhesus macaques and common marmosets (*Callithrix geoffreyi*), cortisol expression in response to a social stressor (separation from mother) was typically consistent throughout the development of infants into juveniles (from 6 months to 18 and 12 months respectively; Higley et al, 1992; French et al, 2012).

4.1.1 Aims

The aforementioned primate studies were conducted in captivity. Non-invasive methodologies now allow the monitoring of physiological stress in wild primates (section 1.3; Hodges & Heistermann, 2003). The current project examines the connections between personality, life history and physiological stress in wild primates using wild Barbary macaques as a study species. The major research question of this chapter is: ***"Is there evidence for the state-dependent adaptive model of personality in wild Barbary macaques?"***

Neuroendocrinology has been proposed as a personality-generating state (Sih et al, 2004; Carere et al, 2010; Duckworth & Sockman, 2012; Wolf & Weissing, 2010); therefore the first aim of this chapter is to confirm this by identifying whether physiological stress measures demonstrate both inter-individual variation and intra-individual consistency. Seven putative personality constructs have been quantified in wild Barbary macaques (chapter 3). These constructs and stress physiology measures will be used to answer the main research question for this chapter:

Q1: ***Is physiological stress related to the expression of personality constructs?***

Q2: ***Is life history status (sex, rank and age) related to the expression of personality constructs?***

Q3: ***Where the expression of a personality construct is related to both stress and life history, is there a relationship between these factors?***

4.2 Methods

4.2.1 Quantifying Personality Constructs

Full details on the methods used for quantifying personality are in Chapter 3. Table 4.1 recaps the personality constructs, the methods used to quantify them and the variables generated for each individual. Behavioural and fGC data were divided into three time blocks based on mating season and chronological order (see table 2.7 and section 2.4.3). For behavioural coding constructs, a score for each personality construct for each time period of data collection could be obtained. Personality constructs derived solely from subjective trait rating, were not quantified concurrently with behavioural and faecal data collection. Therefore, for these constructs, only an overall mean score for these personality constructs can be related to rank, age and fGC variables. For experimental assays, for many subjects, experiments were not equally distributed throughout the data collection timeblocks, therefore, an overall mean is used per subject. Table 4.1 describes how data and faecal sample collection were segregated into time blocks for data analyses, (for full details and justifications of this data segregation, refer to section 2.4.3).

Table 4.1: Barbary macaque personality types, how they were quantified, and variables generated. For full details on the time block segregation of data, refer to table 3.2.

Personality	Method of quantification	Variables generated per individual
Excitability	Product of Excitability$_{TR}$ and Excitability$_{BC}$ scores, generated by trait raiting and behavioural coding respectively	1 score per data collection time block (i.e. 3 per subject)
Sociability	Product of Friendly$_{TR}$ and Sociability$_{BC}$ scores, generated by trait raiting and behavioural coding respectively	
Tactility	Behavioural coding	
Confidence	Trait rating	1 overall mean score
Introversion		
Boldness	Experimental assay	1 overall mean score
Exploration		

4.2.2 Quantifying Physiological Stress

876 faecal samples were collected (see section 2.7.1 for details on collection and storage protocols), aiming for one sample per individual every six days (see Table 4.2 for sampling per individual per time block and per every six days). All samples were at least 5 days apart.

Table 4.2: Sampling frequency for faecal samples in the three sample/data collection time blocks.

	Time block 1 Mating	Time block 2 Inter-mating-birth 1	Time block 3 Inter-mating-birth 2
Green Group Mean # of samples per individual per time block (±SD)	13.87 (±1.06)	7.87 (±0.35)	12.4 (±1.24)
Mean # of samples per individual per every 6 days (±SD)	0.94 (±0.06)	0.78 (±0.06)	1.00 (±0.09)
Blue Group Mean # of samples per individual per time block (±SD)	13.50 (±4.67)	4.67 (±1.15)	12.17 (±1.47)
Mean # of samples per individual per every 6 days (±SD)	0.56 (±0.08)	1.00 (±0.13)	0.97 (±0.12)

Faecal glucocorticoid (fGC) concentrations were calculated from enzyme immunoassay values by standardising for dry faecal weight, dilution and extraction efficiency (details on the methods in section 2.5). For the overall study period and for each time block, mean fGC concentrations for each individual were calculated as a measure of overall physiological stress level. A coefficient of variation in fGC expression (fGCcv) was also calculated as a measure of reactivity using the following equation:

$$fGCcv\ (\%) = \frac{\text{standard deviation fGC}}{\text{mean}\ fGC}\ x\ 100$$

fGCcv was calculated for each individual for each behavioural data collection time block (i.e. calculated using mean and standard deviation values for an individual's samples collected within that time block), as well as an overall value (i.e. calculated using mean and standard deviation values for an individual's samples collected throughout the whole study period). fGCcv is a measure of demonstrated reactive scope (MacLarnon et al, 2015), with higher values indicating greater variation in fGC expression over the study period.

4.2.3 Quantifying Life History Characteristics

Social status

Rank calculations were based on 1,236 dyadic agonistic interactions between subjects observed between 09/10/13-18/04/15 during focal samples and *ad libitum* scans (Altmann, 1974; see chapter 2 for details on behavioural data collection). Calculations were performed using an Elo-rating procedure, which calculates ranks based on the sequence the dyadic interactions occur (Neumann et al, 2011; section 2.5). For each subject, rank was extracted at the end of each data collection time block resulting in three ranks per individual. The starting point for each Elo-rating extraction and calculation was the commencement of data collection (i.e. 09/10/2013). The stability of each hierarchy, *S*, was calculated as the ratio of rank changes per individuals present during the time period (0 = no stability, 1 = completely stable; Neumann et al, 2011). As several dominance hierarchies were included in the analyses (males and females of the Blue group separately analysed; males and females of the Green group separately analysed) Elo rankings for each time block were standardised for each group-sex category to a mean of 0 and a standard deviation of 1 prior to inclusion in statistical models (Yeo & Johnson, 2000; Langos et al, 2015). Elo calculations were performed using the *EloRating* package in R 2.14.1 (Neumann, 2011).

Age

Subjects were categorised by age: primiparous females, adult, and elderly adult (see section 2.3 for definitions). No individuals changed age category during the study period. In females, age was implicitly linked to reproductive state: all primiparous and adult females became pregnant during the study (evidenced by births after the study period). Both of the elderly females failed to reproduce. Thus, in statistical analyses, the interaction between sex and age was sufficient to control for the effects of reproductive cycling (in time block 1, i.e. mating season) and pregnancy (in time blocks 2 and 3, inter-mating-birth seasons).

4.2.4 Statistical Analyses

Physiological Stress as a State

To examine whether individuals varied significantly from each other in terms of fGC concentrations and fGCcv, one-way ANOVAs were conducted with subjects as the factors predicting variation in mean stress values (considered significant when $p<0.05$). To test intra-individual consistency in stress values, the ANOVA-based measure of repeatability (R_A) was used (section 2.9.1).

Subjects were factorial predictors of repeatability for fGC concentrations (calculated from all faecal samples; n=876) and fGCcv values (calculated for each subject in each time block; n=81) across the three time blocks.

Models Examining Relationship between Physiological Stress, Life History and Personality

How personality constructs were derived determined the type of statistical analyses used to explore the relationships between personality, stress and life history (table 4.1). Personality constructs generated from behavioural coding were quantified concurrently with behavioural and faecal data collection. For these constructs, linear mixed-effect models (LMEs) were created using values from each time block (i.e. one value per variable per individual per each of the three time blocks) with individual subjects included as random factors (Pineirho & Bates, 2000). For trait rating- and experimental assay-derived personality constructs, linear regression models were fitted with mean values for all variables, i.e. one value per individual representing the whole study period).

To examine how ***stress*** variables were related to personality construct scores linear regression (for trait rating- and experiment assay-derived personality constructs) and linear mixed-effect models (LMEs; for behavioural coding-derived personality constructs) were used with fGC and fGCcv included as predictors of personality scores.

To examine how ***life history*** was related to personality construct scores, linear regressions (for trait rating- and experiment assay-derived personality constructs) and LMEs (for behavioural coding-derived personality constructs) were used, with sex, rank and age (and all first order interactions) included as predictors of personality scores.

Where stress and life history variables were found to be related to personality construct scores, linear regressions or LMEs (depending on personality and number of scores for that type) were used, with stress and life history variable(s) included as predictors of personality scores. Stress and life history variables were not included in an initial model due to the limitation of a small sample size for certain personality constructs where only one score is available (n=27). Including all variables in the initial model would over-parametrize the model (Zuur et al, 2011). For each model, collinearity of fixed factors was examined using variance inflation factors (VIF) with a cut-off value of 2.0 (Field et al, 2012).

Model Selection and Significance Testing

For each model, backwards model selection was performed using Akaike's information criterion (AIC) and maximum likelihood optimisation to identify the best fit models, which were then subjected to Wald regression analyses. See section 2.9.2 for full details on model selection methods.

4.3 Results

4.3.1 Data exploration

Analyses of collinearity revealed sex to be collinear with other fixed variables (VIF >2.0; all VIFs reported in tables A9a and A9a in Appendix A9). Therefore, males and females were analysed in separate models. Table 4.3 outlines descriptive statistics and Shapiro Wilks test for normality of personality construct scores for each sex. All personality score variables were normally distributed with the exception of Excitability and Confidence in females; $\log_{10}$ transformation achieved a normal distribution for Excitability (Shapiro

Wilk=0.96, df=45, p=0.16) and Confidence (Shapiro Wilk=0.90, df=15, p=0.08).

Table 4.3: Descriptive statistics and tests of normality for personality score variables.

Overall mean values	N	Mean	Min	Max	St Dev	Shapiro-Wilk statistic	*p*
Confidence							
♂	12	3.91	3.19	5.01	0.51	0.95	0.67
♀	15	3.60	2.57	5.45	0.95	0.90	0.04
Introversion							
♂	12	3.50	2.00	5.50	1.06	0.96	0.81
♀	15	2.48	1.13	4.17	0.94	0.95	0.55
Boldness							
♂	12	0.78	0.33	1.42	0.33	0.89	0.15
♀	15	0.85	0.25	1.49	0.34	0.95	0.45
Exploration							
♂	12	0.58	0.24	0.98	0.23	0.96	0.74
♀	15	0.50	0.16	1.03	0.26	0.94	0.37
Excitability							
♂	36	2.54	0.85	4.50	1.07	0.96	0.18
♀	45	0.84	0.29	2.17	0.46	0.89	<0.01
Sociability							
♂	36	1.16	0.29	1.73	0.35	0.95	0.06
♀	45	1.19	0.54	1.76	0.32	0.98	0.43
Tactility							
♂	36	0.46	0.04	0.80	0.17	0.96	0.25
♀	45	0.74	0.07	1.10	0.21	0.96	0.16

4.3.2 Sex differences in personality expression

Following the decision to analyse male and female personality expression in separate models, one-way ANOVAs (with repeated measures for personality variables with three time block values) were performed to examine sex differences in the expressions of the different personality constructs. Table 4.4 lists the results: males had significantly higher Excitability and Introversion scores than female; females had significantly higher Tactility scores than males (figure 4.1).

Table 4.4: Results of ANOVAs comparing personality construct scores between males and females. Personality scores which differed significantly according to sex are in bold.

Personality	F	df	*p*
Excitability	**20.14**	**1,25**	**<0.01**
Sociability	0.84	1,25	0.73
Tactility	**18.85**	**1,25**	**<0.01**
Confidence	1.05	1,26	0.32
Introversion	**7.08**	**1,26**	**0.01**
Boldness	0.27	1,26	0.61
Exploration	0.65	1,26	0.43

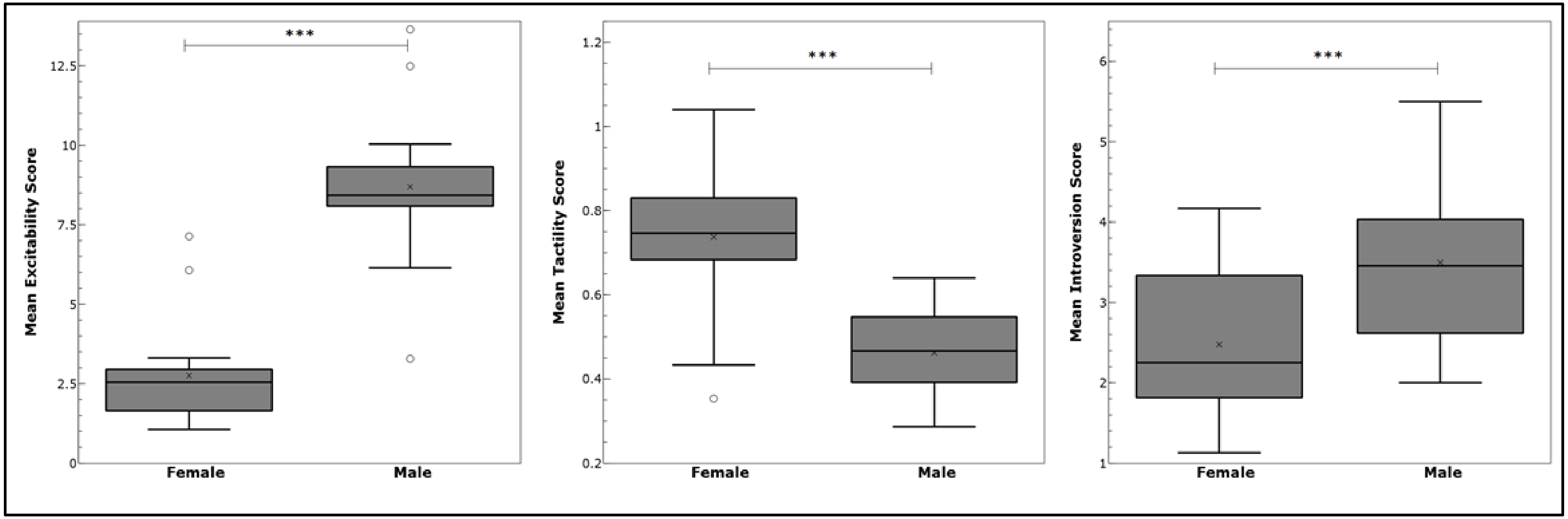


Figure 4.1: Median values (central lines in boxes) and 25% percentiles (box edges) for male and female mean (a) Excitability scores (b) Tactility scores and (c) Introversion scores. For all plots, n=27 (males n=12, females n=15). Circles represent outliers and crosses mean values.

4.3.3 Physiological Stress as a State

Intra-individual consistency and inter-individual variation in physiological stress levels were observed. Both stress physiology measures varied significantly between individuals (table 4.5). Individuals demonstrated consistent fGC concentrations across the three time blocks (R_A=0.19; CI=0.08-0.29; p<0.01); however, individuals did not demonstrate consistent fGCcv values for the same periods (R_A=0.06; CI=-0.18-0.31; p=0.27)

Table 4.5: Results of one-way ANOVA examining whether individuals varied significantly in their mean fGC concentrations and fGCcv. Significant results are in bold.

Variable	F	df	*p*
fGC	**10.81**	**1,26**	**<0.01**
fGCcv	**2.96**	**1,26**	**<0.01**

Figure 4.2 illustrates variation between and within subjects for the fGC concentrations of all samples collected (n=876). Visual inspection of the data suggested differences between the two groups and sexes. Repeated measures ANOVAs were performed comparing mean fGC concentration and fGCcv (one value per time block per subject) with sex and group as factorial predictors of variation. Results confirmed significant effects of sex and group on mean fGC concentration (table 4.6). This, with the previous VIF analysis, supported analysing the sexes separately in different models. The Blue group had significantly higher mean fGC concentrations; females had higher fGC concentrations than males. There were no sex differences in fGCcv, but a trend

(p=0.06) for the Blue group to have higher fGCcv values than the Green group. Based on these findings, for the LME analyses, subjects were nested in groups; for the linear models, interactions with group were included to control for group differences.

Table 4.6: Results of repeated measure ANOVAs comparing stress physiology variables between groups and sexes. Significant results are in bold.

Factor	Variable	F	df	*p*
Group	**fGC**	**16.89**	**1,25**	**<0.01**
	fGCcv	3.67	1,25	0.06
Sex	**fGC**	**9.99**	**1,25**	**<0.01**
	fGCcv	2.71	1,25	0.11

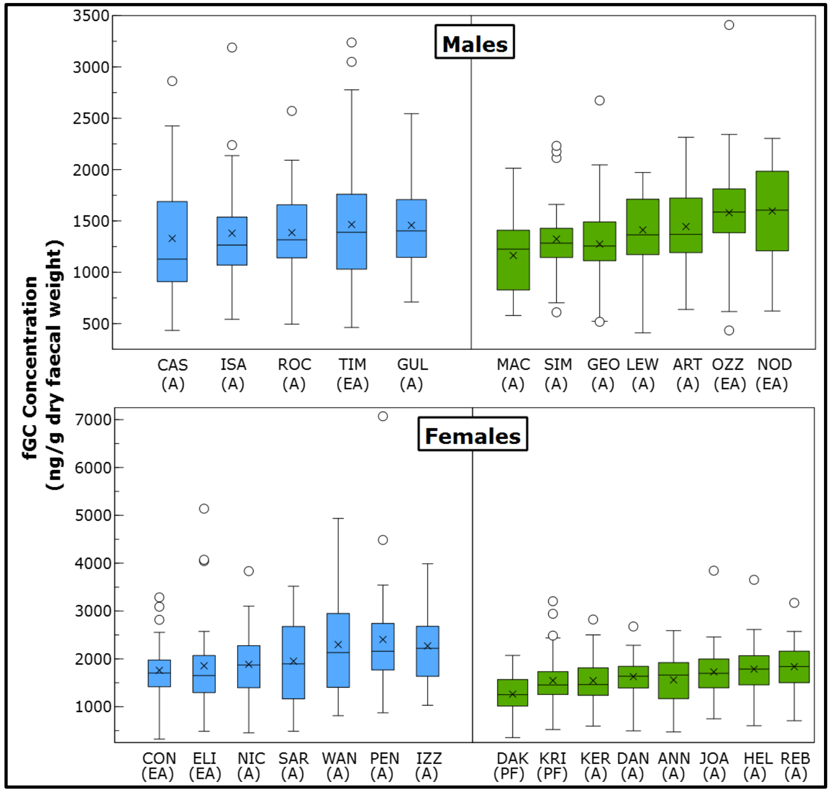


Figure 4.2: Median values (central lines of boxes) and 25% percentiles (edges of boxed) of fGC concentrations of samples for each subject (n=27 subjects, n=876 samples, mean number of samples per individual = 32.44[±2.67]). Plots are segregated by group (Blue on left [shaded blue] and Green on right [shaded green]) and sex (males top, females bottom). Subject names are listed on the X-axis with age category in parentheses (PF = primiparous females, A = adult, EA = elderly adult). Subjects are ordered horizontally by increasing mean fGC concentration (mean indicated by crosses; circles indicate outliers).

4.3.4 Rank and Age Distribution of Subjects

Dominance hierarchies showed a strong degree of stability within time blocks, with *S* ranging from 0.98 to >0.99, with a mean of 0.99. Rank positions for individuals for each of the data collection time blocks are listed in table 4.7, along with each subject's age category during the study period.

Table 4.7: Ages and ranks for subjects for each time block. Where rank changes between time blocks occurred, the changes in position within hierarchy are in parentheses besides the rank position. *S* indicates the stability of the hierarchies within the time blocks (0 = no stability; 1 = completely stable).

Green Group	Age	Sex	Rank 1: Mating	Rank 2: Inter-mating-birth	Rank 3: Inter-mating-birth
ANN	Adult	♀	1	1	7 (-6)
DAK	Sub-adult	♀	8	8	5 (+3)
DAN	Adult	♀	7	7	6 (+1)
HEL	Adult	♀	6	6	4 (+2)
JOA	Adult	♀	2	3 (-1)	8 (-5)
KER	Adult	♀	3	2 (+1)	2
KRI	Sub-adult	♀	5	5	3 (+2)
REB	Adult	♀	4	4	1 (+3)
			S = 0.99	*S* = 0.99	*S* = 0.98
ART	Adult	♂	2	1 (+1)	1
GEO	Adult	♂	4	4	5 (-1)
LEW	Adult	♂	5	3 (+2)	6 (-3)
MAC	Adult	♂	7	7	4 (+3)
NOD	Elderly adult	♂	3	6 (-3)	7 (-1)
OZZ	Elderly adult	♂	1	2 (-1)	3 (-1)
SIM	Adult	♂	6	5 (+1)	2 (+3)
			S = 0.98	*S* = 0.99	*S* = 0.99
Blue Group					
CON	Elderly adult	♀	2	2	2
ELI	Elderly adult	♀	5	5	5
IZZ	Adult	♀	4	3 (+1)	3
NIC	Adult	♀	3	4 (-1)	4
PEN	Sub-adult	♀	7	7	7
SAR	Adult	♀	1	1	1
WAN	Adult	♀	6	6	6
			S = 0.99	*S* >0.99	*S* >0.99
CAS	Adult	♂	5	4 (+1)	4
GUL	Adult	♂	4	2 (+2)	1 (-1)
ISA	Adult	♂	2	1 (+1)	2(+1)
ROC	Adult	♂	3	3	3
TIM	Elderly adult	♂	1	5 (-4)	5
			S = 0.97	*S* = 0.99	*S* = 0.98

4.3.5 Physiological Stress and Personality Expression

For LMEs, the full models were:

Personality ≈ fGC + fGCcv + (subjects nested in group as random effect)

For linear regressions, the full models were:

Personality ≈ fGC +fGCcv + Group + fGC*Group + fGCcv*Group

Following model selection procedure, only best fit models found to be significantly different from null models are discussed below. Tables A10a and A10b in Appendix A10 list the best fit models relating personality scores to physiological stress where the best fit models did not differ significantly from the null models for males and females respectively.

Of the seven best fit models examined for males, two were significantly different from the null model (table 4.8). Of the seven best fit models examined for females, two were significantly different from the null model (table 4.8).

Table 4.8: Results of likelihood ratio tests, comparing best fit models to null models when examining the relationship between personality construct scores and stress measures (fGC concentration and fGCcv). Models which differed significantly from null models are in bold.

Personality	F	df	p
♂			
Excitability	**4.23**	**1**	**0.04**
Sociability	0.26	1	0.61
Tactility	**6.95**	**1**	**0.01**
Confidence	1.24	3	0.29
Introversion	1.24	5	0.39
Boldness	0.56	1	0.47
Exploration	0.68	3	0.59
♀			
Excitability	0.02	1	0.90
Sociability	0.32	1	0.57
Tactility	**3.89**	**1**	**<0.05**
Confidence	1.74	3	0.22
Introversion	0.29	1	0.60
Boldness	2.31	4	0.13
Exploration	**6.23**	**3**	**0.01**

Males

Table 4.9 lists the best fit models examining the relationships between male Excitability and Tactility scores and stress measures. **Excitability** scores were related to fGCcv, with model estimates predicting individuals with higher variation in cortisol expression had higher Excitability scores than individuals with lower variation in cortisol expression (figure 4.3). **Tactility** scores were also found to be related to fGCcv, with model estimates predicting individuals with higher variation in cortisol expression had lower Tactility scores than individuals with lower variation in cortisol expression (figure 4.4).

Table 4.9: Best fit models used to describe relationship between male (a) Excitability and (b) Tactility scores and stress measures (fGC concentration and fGCcv). AIC for all models are reported; ΔAIC between the full and best fit models are reported, with ΔAIC between each model and the next best model in parentheses. Significant relationships are in bold.

Males (a)					AIC	ΔAIC
Full model	*Excitability ~ fGC + fGCcv + (subjects nested in group as random effect)*				194.52	
Best fit model	*β*	SE	Wald	*p*	192.52	2.00 (2.00)
Intercept	5.42	1.72	134.40	<0.01		
fGCcv	**0.09**	**0.05**	**4.30**	**<0.05**		
(b)					AIC	ΔAIC
Full model	*Tactility ~ fGC + fGCcv + (subjects nested in group as random effect)*				-22.55	
Best fit model	*β*	SE	Wald	*p*	-24.40	1.85 (1.85)
Intercept	0.68	0.08	322.60	<0.01		
fGCcv	**-0.01**	**<0.01**	**7.50**	**0.01**		
Second best model					-22.55	
Intercept	0.61	2.87	314.42	<0.01		
fGC	<0.01	0.71	1.00	0.33		
fGCcv	**-0.01**	**<0.01**	**6.44**	**0.02**		

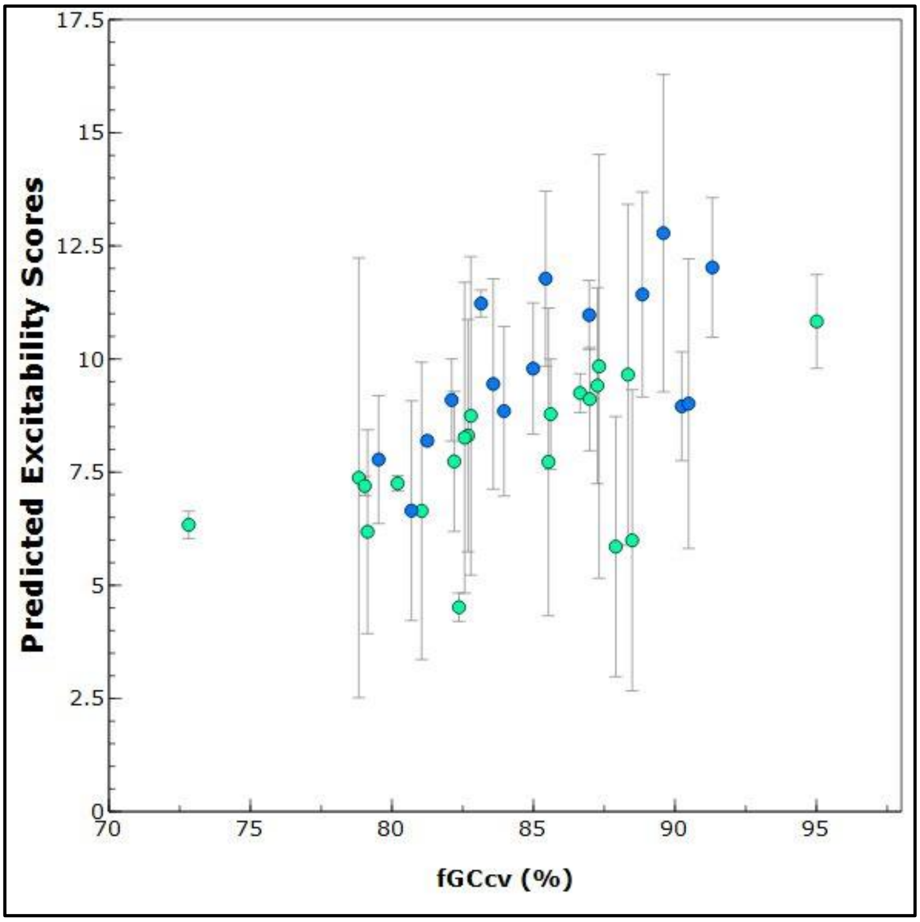


Figure 4.3: Plot of the predicted relationship between male Excitability scores and fGCcv based on the model described in table 4.10. Error bars represent residual values. All plots (n=36) are coloured to indicate group:

● for Blue group; ● for Green group

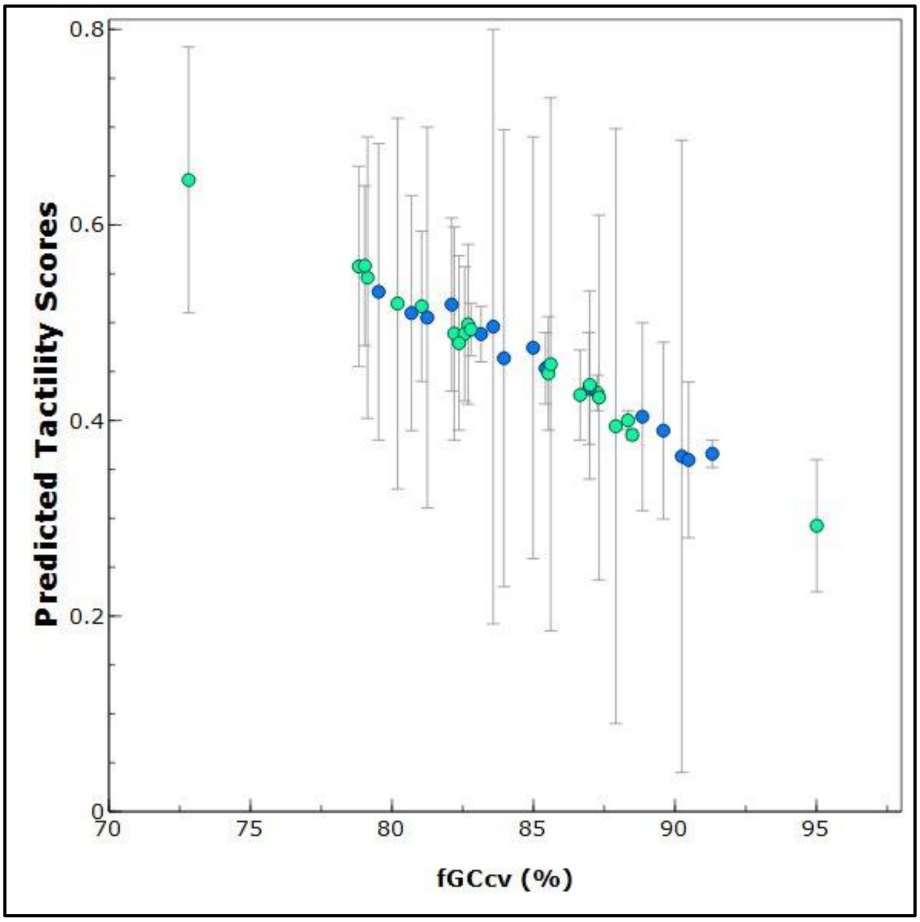


Figure 4.4: Plot of the predicted relationship between male Tactility scores and fGCcv based on the model described in table 4.10. Error bars represent residual values. All plots (n=36) are coloured to indicate group:

● for Blue group; ● for Green group.

Females

Table 4.10 lists the best fit models examining the relationships between female Tactility and Exploration scores and stress measures. **Tactility** scores were related to mean fGC concentrations, with model estimates suggesting individuals with higher fGC concentrations had higher Tactility scores than individuals with lower fGC concentrations (figure 4.5). However, in both the best fit and second best fit models, this relationship only approached significance (p=0.06). **Exploration** scores were related to the interaction between group (Blue females had higher Exploration scores than Green females) and fGC concentration, with model estimates suggesting that in both groups, individuals with higher fGC expression had higher Exploration scores than individuals with lower fGC expression (table 4.6).

Table 4.10: Best fit models used to describe relationship between female (a) Tactility and (b) Exploration scores and stress measures (fGC concentration and fGCcv). AIC for all models are reported; ΔAIC between the full and best fit models are reported, with ΔAIC between each model and the next best model in parentheses. Significant relationships are in bold.

Females (a)					AIC	ΔAIC
Full model	*Tactility ~ fGC + fGCcv + (subjects nested in group as random effect)*				-14.83	
Best fit model	*β*	SE	Wald	*p*	-16.68	1.85 (1.85)
Intercept	0.50	0.13	275.43	<0.01		
fGC	<0.01	<0.01	3.90	0.06		
Second best model					-14.83	
Intercept	0.46	0.16	262.60	<0.01		
fGC	<0.01	<0.01	3.84	0.06		
fGCcv	<0.01	<0.01	0.15	0.70		

(b)					AIC	ΔAIC
Full model	*Exploration ~ fGC +fGCcv + Group + fGC*Group + fGCcv*Group*				-44.02	
Best fit model	*β*	SE	Wald	*p*	-47.87	3.85 (1.87)
Intercept	-4.14	1.31	-	-		
fGC	**<0.01**	**<0.01**	**7.54**	**0.02**		
Group	**2.18**	**0.79**	**6.18**	**0.03**		
fGC:Group	**<0.01**	**<0.01**	**5.09**	**0.04**		
Second best model					-46.00	
Intercept	-4.08	1.38	-	-		
fGC	**<0.01**	**<0.01**	**6.91**	**0.03**		
fGCcv	<-0.01	0.01	0.41	0.54		
Group	**2.24**	**0.85**	**5.41**	**0.04**		
fGC:Group	<0.01	<0.01	4.61	0.06		

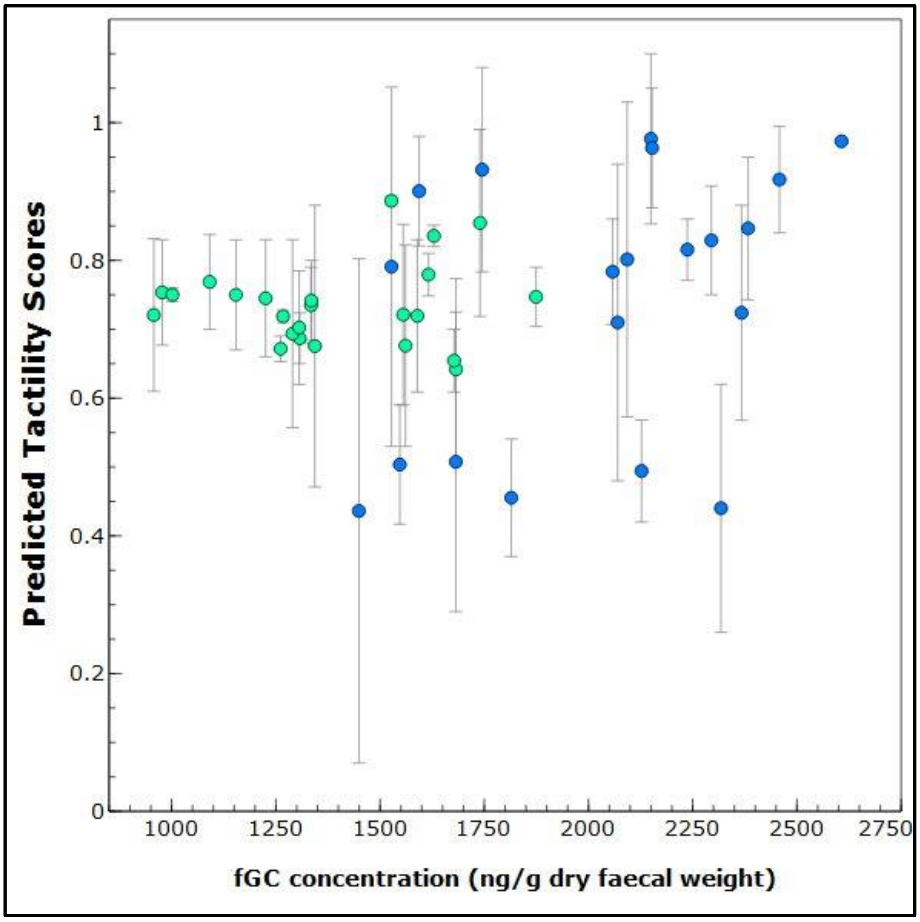


Figure 4.5: Plot of the predicted relationship between female Tactility scores and fGC concentration based on the model described in table 4.11. Error bars represent residual values. All plots (n=45) are coloured to indicate group:

● for Blue group; ● for Green group

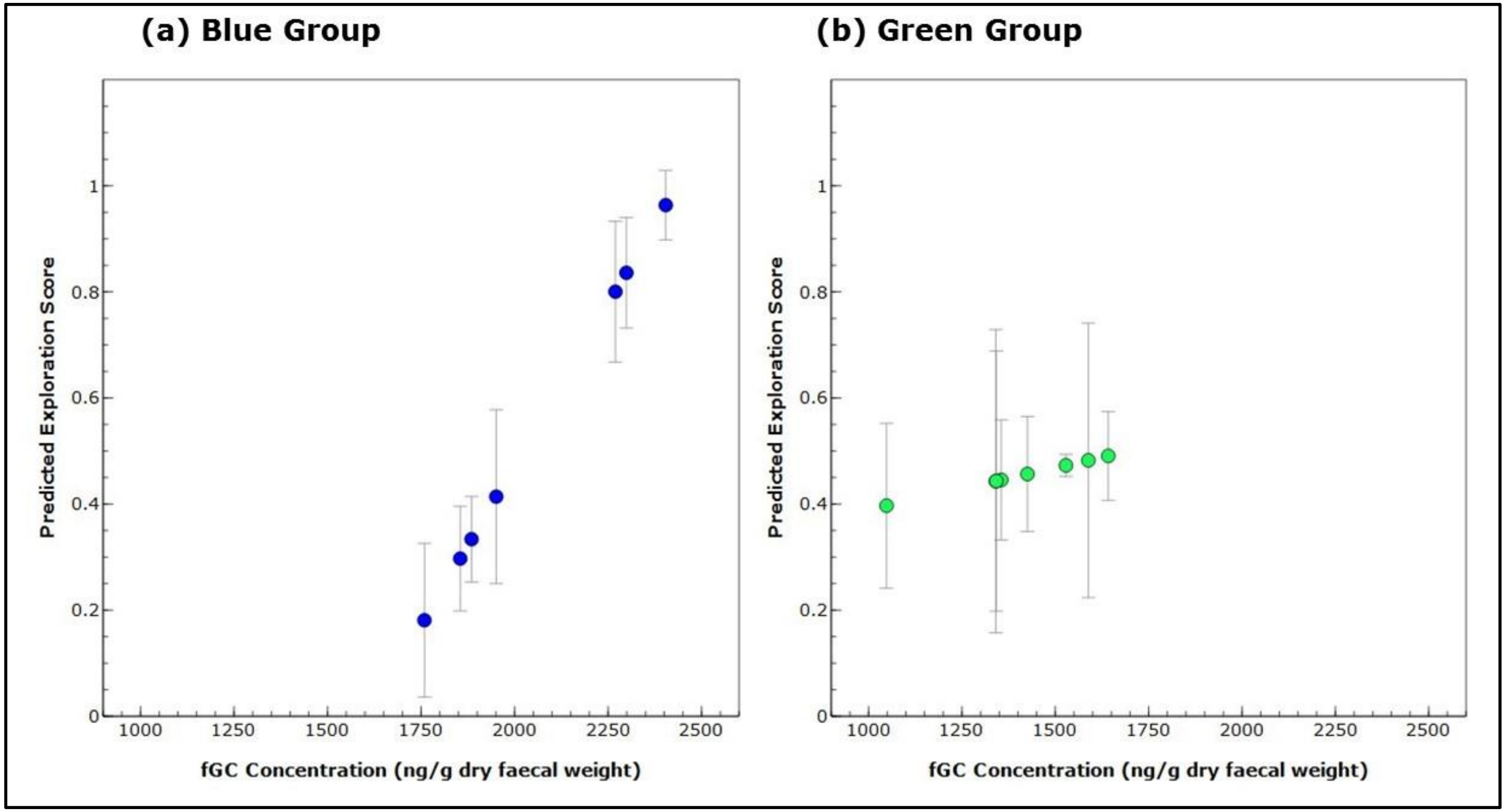


Figure 4.6: Plot of the predicted relationship between female Exploration scores and the interaction between fGC concentration and group based on the model described in table 4.11. Error bars represent residual values. All plots (n=15) are coloured to indicate group: ● for Blue group; ● for Green group

4.3.6 Life History and Personality Expression

For LMEs, the full models were:

Personality ≈ Rank + Age + Rank*Age + (subjects nested in group as random effect)

For linear regressions, the full models were:

Personality ≈ Rank + Age + Group + Rank*Age + Rank*Group + Group*Age

Following model selection procedure, only best fit models found to be significantly different from null models are discussed below. Tables A10c and A10d in Appendix A10 list the best fit models relating personality scores to life history measures where the best fit models did not differ significantly from the null models for males and females respectively.

Of the seven best fit models examined for males, two were significantly different from the null model (table 4.11). Of the seven best fit models examined for females, three were significantly different from the null model (table 4.11).

Table 4.11: Results of likelihood ratio tests, comparing best fit models to null models when examining the relationship between personality construct scores and life history measures (rank and age). Best fit models differing significantly from the null model are in bold.

Personality	F	df	p
♂			
Excitability	**3.88**	**1**	**<0.05**
Sociability	0.22	1	0.64
Tactility	**18.11**	**3**	**<0.01**
Confidence	1.43	4	0.32
Introversion	1.20	5	0.41
Boldness	3.41	5	0.08
Exploration	3.37	4	0.08
♀			
Excitability	0.26	1	0.61
Sociability	**20.72**	**3**	**<0.01**
Tactility	**5.24**	**1**	**0.02**
Confidence	**10.86**	**4**	**<0.01**
Introversion	1.49	5	0.28
Boldness	3.36	4	0.05
Exploration	2.29	5	0.13

Males

Table 4.12 lists the best fit models examining the relationships between male Excitability and Tactility scores and life history measures. The best fit model found a relationship between **Excitability** scores and age, with model estimates suggesting elderly adults had lower Excitability scores than adults. However, this relationship was not significant in the second best fit model and, therefore, not considered significantly supported. **Tactility** scores were related to the interaction between rank and age, with model estimates suggesting that, overall, low ranking individuals had lower Tactility scores than high ranking individuals. However, the interaction of age with rank revealed that within elderly adults, low ranking elderly adults tended to have higher Tactility scores than high ranking elderly adults (figure 4.7).

Table 4.12: Best fit models used to describe relationships between male (a) Excitability and (b) Tactility scores and life history measures (rank and age). ΔAIC is reported between the full and best fit models, with ΔAIC between each model and the next best model in parentheses. Significant relationships are in bold.

Males (a)					AIC	ΔAIC
Full model	*Excitability ~ Rank + Age + Rank*Age + (subjects nested in group as random effect)*				197.63	
Best fit model	β	SE	Wald	*p*	194.87	2.76 (0.84)
Intercept	5.42	1.72	134.40	<0.01		
Age	**-0.09**	**0.05**	**4.30**	**<0.05**		
Second best model					195.71	1.92
Intercept	15.75	3.69	155.88	<0.01		(0.08)
Rank	0.64	0.61	1.04	0.32		
Age	-3.14	1.61	3.80	0.08		

(b)					AIC	ΔAIC
Full model	*Tactility ~ Rank + Age + Rank*Age + (subjects nested in group as random effect)*				31.56	
Best fit model	β	SE	Wald	*p*	31.56	0.00 (0.00)
Intercept	0.69	0.13	361.49	<0.01		
Rank	0.47	0.12	1.18	0.29		
Age	-0.10	0.06	2.93	0.12		
Rank:Age	**0.21**	**0.05**	**16.81**	**<0.01**		

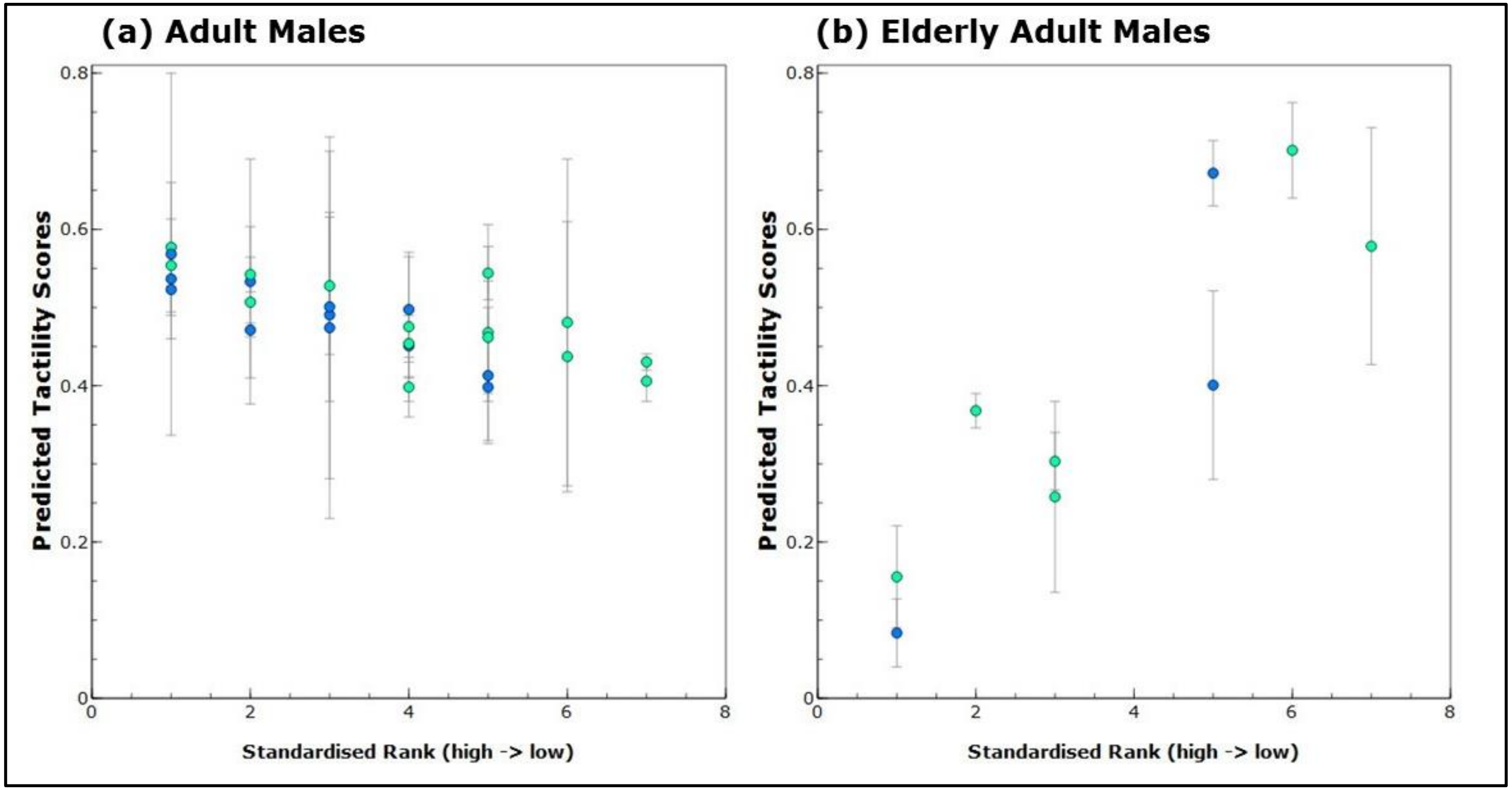


Figure 4.7: Plot of the predicted relationship between male Tactility scores and the interaction between rank and age based on the model described in table 4.13. Error bars represent residual values; plots are sized to indicate age (see inset). All plots (n=36) are coloured to indicate group:

● for Blue group; ● for Green group

Females

Table 4.13 lists the best fit models examining the relationships between female Sociability, Tactility and Confidence scores and life history measures. **Sociability** scores were related to the interaction between rank and age, with model estimates suggesting high ranking individuals had higher Sociability scores than low ranking individuals in all age groups; Sociability scores were also related to the interaction between rank and age, with steeper declines in Sociability associated with lower ranks in adult females compared to primiparous females, and with elderly females compared to both primiparous and adult females (figure 4.8). **Tactility** scores were related to age, with model estimates suggesting increasing age was associated with lower Tactility scores. This relationship remained significant in the second best fit model. **Confidence** scores were related to the interaction between group and rank: for Green group females, low ranking females tended to have higher Confidence scores than high ranking inividuals, for Blue group females, low ranking individuals tended to have lower Confidence scores than high ranking individuals (figure 4.9).

Table 4.13: Best fit models used to describe relationship between female (a) Sociability, (b) Tactility and (c) Confidence scores and life history measures (rank and age). ΔAIC is reported between the full and best fit models, with ΔAIC between each model and the next best model in parentheses. Significant relationships are in bold.

Females (a)					AIC	ΔAIC
Full model	*Sociability ~ Rank + Age + Rank*Age + (subjects nested in group as random effect)*				144.76	
Best fit model	*B*	SE	Wald	*p*	144.76	0.00 (0.00)
Intercept	5.98	0.68	652.85	<0.01		
Rank	**0.91**	**0.87**	**28.51**	**<0.01**		
Age	-0.60	0.34	3.61	0.08		
Rank:Age	**-1.01**	**0.44**	**5.33**	**0.03**		
(b)					AIC	ΔAIC
Full model	*Tactility ~ Rank + Age + Rank*Age + (subjects nested in group as random effect)*				-14.09	
Best fit model	*B*	SE	Wald	*p*	-18.03	3.94 (1.99)
Intercept	1.05	0.13	370.98	<0.01		
Age	**-0.16**	**0.07**	**5.99**	**0.03**		
Second best model					-16.04	
Intercept	1.05	0.14	357.11	<0.01		
Rank	<0.01	0.03	0.18	0.67		
Age	**-0.16**	**0.07**	**5.60**	**0.03**		
(c)					AIC	ΔAIC
Full model	*Confidence ~ Rank + Age + Group + Rank*Age + Rank*Group + Group*Age*				-78.64	
Best fit model	*B*	SE	Wald	*p*	-82.33	3.69 (1.71)
Intercept	0.47	0.08	-	-		
Rank	-0.31	0.05	2.65	0.13		
Age	0.04	0.03	3.41	0.09		
Group	<-0.01	0.03	0.10	0.76		
Rank:Group	**0.19**	**0.03**	**37.27**	**<0.01**		
Second best model					-80.62	
Intercept	0.54	0.18	-	-		
Rank	-0.31	0.05	2.43	0.15		
Age	0.01	0.08	3.13	0.11		
Group	-0.05	0.12	0.09	0.77		
Rank:Group	**0.19**	**0.03**	**34.21**	**<0.01**		
Age:Group	0.03	0.06	0.18	0.68		

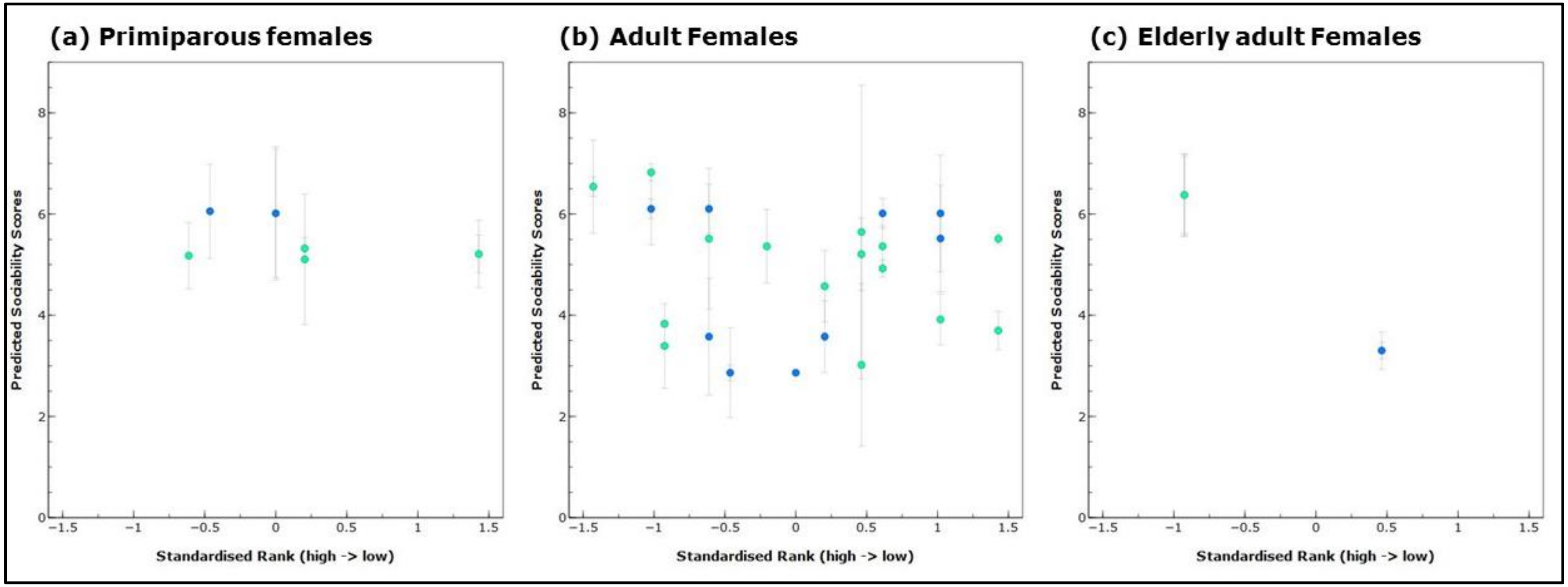


Figure 4.8: Plot of the predicted relationship between female Sociability scores and the interaction between rank and age based on the model described in table 4.14. Error bars represent residual values. All plots (n=45) are coloured to indicate group:

● for Blue group; ● for Green group

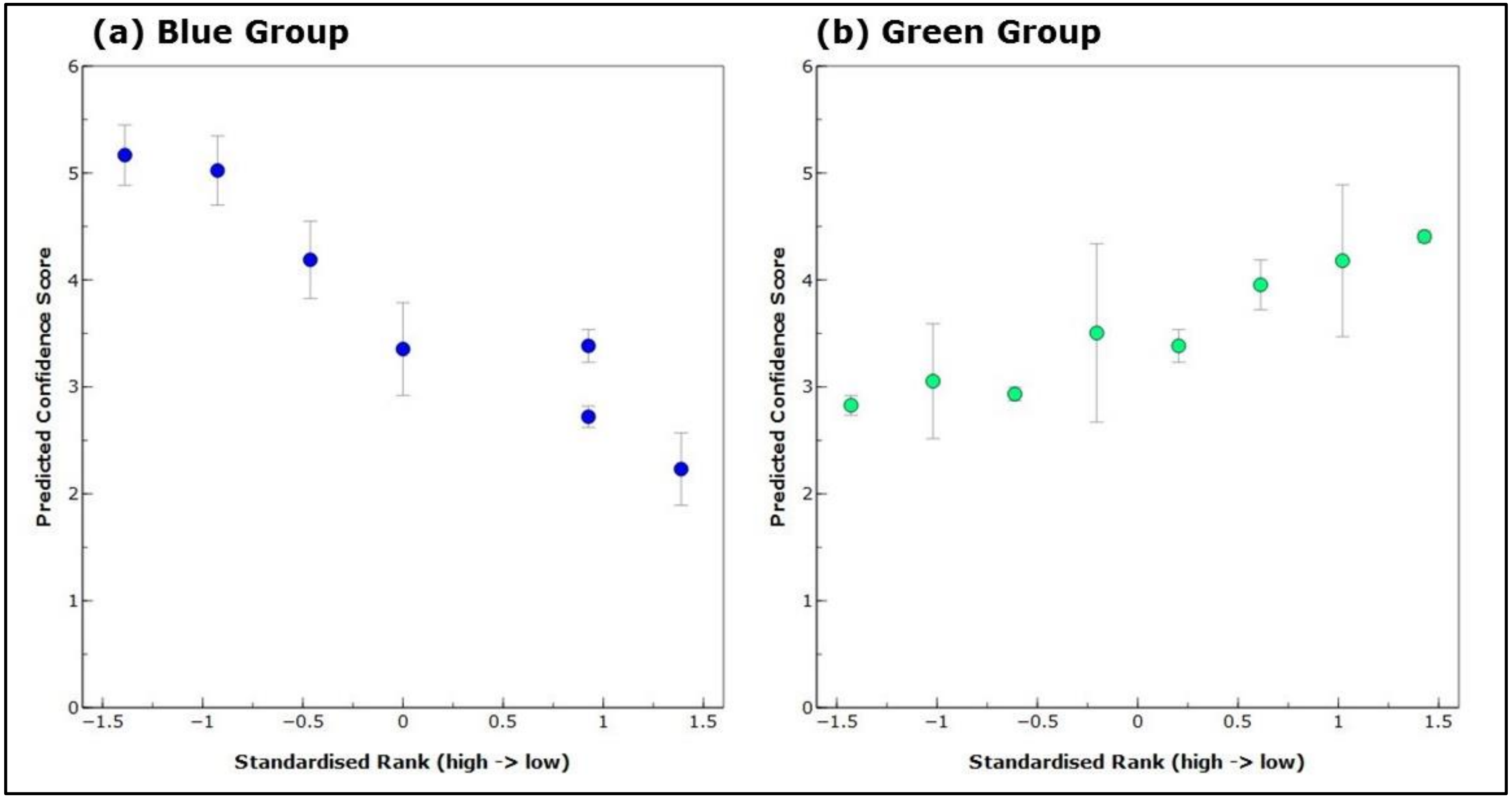


Figure 4.9: Plot of the predicted relationship between female Confidence scores and the interaction between group and rank based on the model described in table 4.14. Error bars represent residual values. All plots (n=15) are coloured to indicate group:

● for Blue group; ● for Green group

4.3.7 Relationships between Physiological Stress, Life History Stage and Personality Expression

For both males and females, only Tactility was found to be related to both physiological stress (for females, the relationship between Tactility scores and fGC expression was near significant [p=0.06]) and life history measures. Best fit models exploring physiological stress, life history and Tactility differed significantly from null models for both sexes (table 4.14).

Table 4.14: Results of likelihood ratio tests, comparing best fit models to null models when examining the relationship between Tactility construct scores and combined stress and life history measures. Best fit models differing significantly from the null model are in bold.

Personality	X^2	df	p
♂			
Tactility	**18.11**	**3**	**<0.01**
♀			
Tactility	**5.24**	**1**	**0.02**

Males

Table 4.15 lists the best fit models examining the relationships between male Tactility scores, stress reactivity and life history measures. **Tactility** scores were related to the interaction between fGCcv and age, with model estimates suggesting that higher fGCcv was associated with lower Tactility scores and in elderly adult males, higher fGCcv was associated with lower Tactility scores than higher fGCcv in adult males (figure 4.10). This relationship remained significant in the second best fit model.

Tactility scores were also related to the interaction between rank and age, with model estimates suggesting that, whilst overall, low ranking individuals had lower Tactility scores than high ranking individuals. In elderly adults, the inverse relationship existed so that low ranking elderly adults tended to have higher Tactility scores than high ranking elderly adults (refer to figure 4.7).

Table 4.15: Best fit models used to describe relationship between male Tactility scores and combined stress and life history stage measures. ΔAIC is reported between the full and best fit models, with ΔAIC between each model and the next best model in parentheses. Significant relationships are in bold.

Males					AIC	ΔAIC
Full model	*Tactility ~ fGCcv + Rank + Age + 1st order interactions + (subjects nested in group as random effect)*				-34.96	
Best fit model	*B*	SE	Wald	*p*	-36.55	1.59 (1.59)
Intercept	0.10	0.41	457.31	<0.01		
fGCcv	**-0.02**	**0.01**	**11.10**	**<0.01**		
Rank	-0.38	0.12	1.52	0.23		
Age	0.24	0.19	2.48	0.15		
fGCcv:Age	**-0.01**	**<0.01**	**6.91**	**0.02**		
Rank:Age	**0.17**	**0.05**	**11.48**	**<0.01**		
Second best model					-34.96	
Intercept	0.06	0.42	487.07	<0.01		
fGCcv	**-0.02**	**0.01**	**11.32**	**<0.01**		
Rank	-0.40	0.13	1.36	0.26		
Age	0.26	0.19	2.61	0.14		
fGCcv:Rank	<0.01	<0.01	1.80	0.20		
fGCcv:Age	**-0.01**	**0.01**	**7.04**	**0.02**		
Rank:Age	**0.16**	**0.05**	**9.53**	**0.01**		

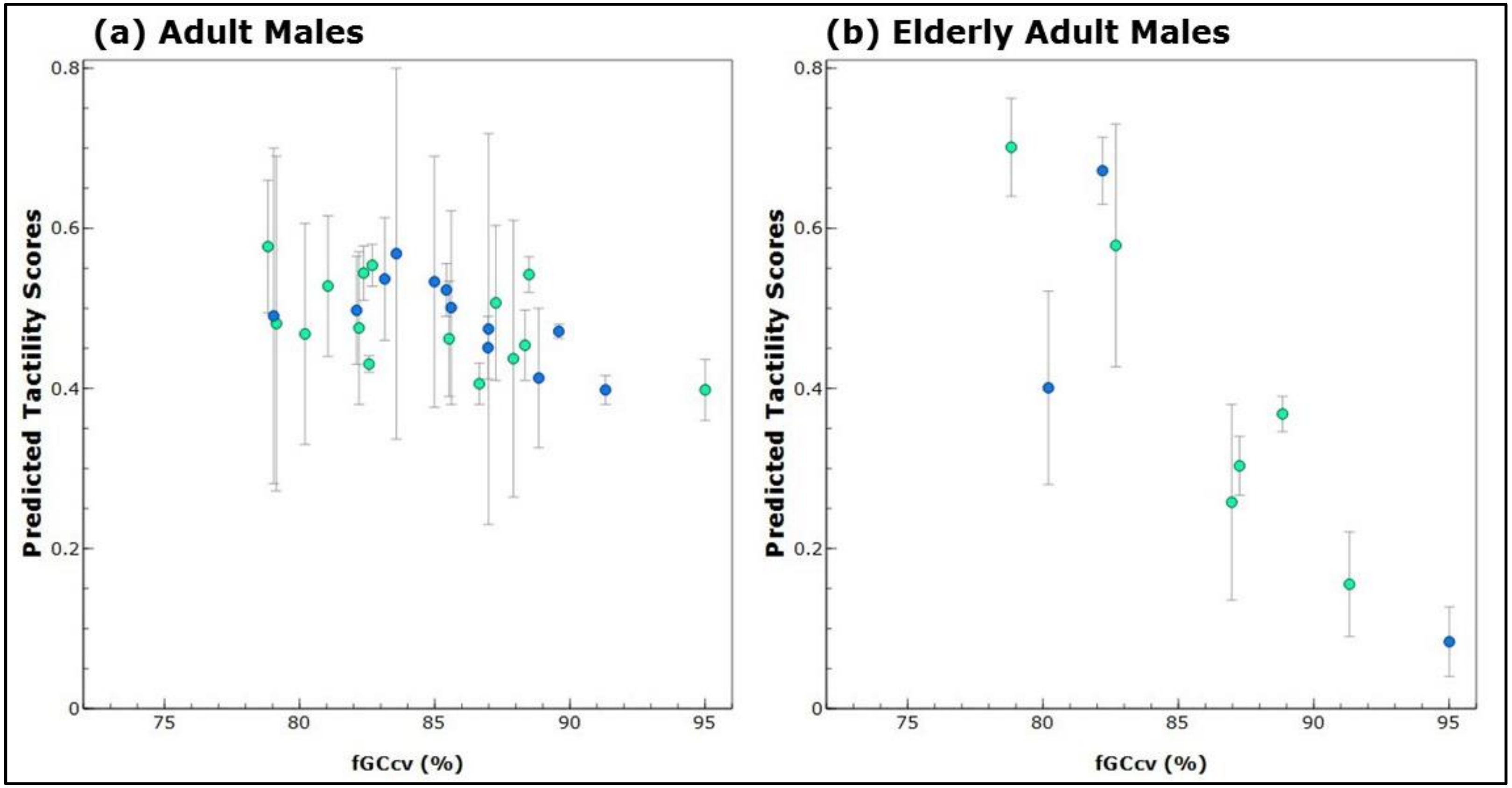


Figure 4.10: Plot of the predicted relationship between male Tactility scores and the interaction between age and fGCcv based on the model described in table 4.15. Error bars represent residual values; plots are sized to indicate age (see inset). All plots (n=36) coloured to indicate group:

● for Blue group; ● for Green group

Females

Table 4.16 lists the best fit models examining the relationships between female Tactility scores, stress reactivity and life history measures. **Tactility** scores were related to age, with model estimates suggesting that elderly adults tended to have lower Tactility scores than primiparous and adult females (figure 4.11). The same model found a relationship between Tactility scores and fGC concentration, with model estimates suggesting increasing fGC concentrations were associated with higher Tactility scores (figure 4.11).

Table 4.16: Best fit models used to describe the relationship between female Tactility scores and combined stress and life history stage measures. ΔAIC is reported between the full and best fit models, with ΔAIC between each model and the next best model in parentheses. Significant relationships are in bold.

Females					AIC	ΔAIC
Full model	*Tactility ~ fGCcv + Rank + Age + 1^{st} order interactions + (subjects nested in group as random effect)*				-16.63	
Best fit model	*B*	SE	Wald	*p*	-23.76	7.13 (1.43)
Intercept	0.82	0.14	491.16	<0.01		
fGC	**<0.01**	**<0.01**	**4.45**	**0.04**		
Age	**-0.20**	**0.06**	**11.58**	**<0.01**		
Second best model				20.62	-22.33	
Intercept	0.81	0.14	554.77	<0.01		
fGC	**<0.01**	**<0.01**	**4.41**	**0.04**		
Rank	-0.02	0.03	0.03	0.87		
Age	**-0.21**	**0.06**	**13.74**	**<0.01**		

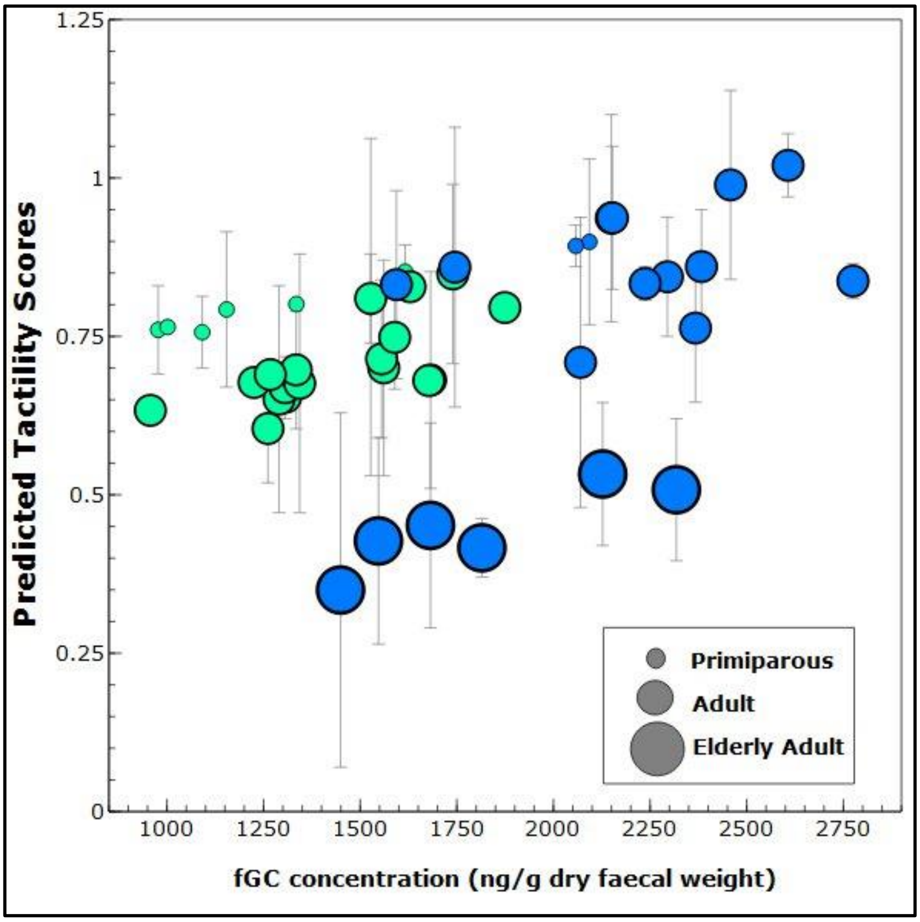


Figure 4.11: Plot of the predicted relationship between female Tactility scores, fGC concentration and age based on the model described in table 4.17. Error bars represent residual values; plots are scaled according to age (see inset). All plots (n=45) are coloured to indicate group:

● **for Blue group;** ● **for Green group**

4.3.8 Summary

- Inter-individual variation and intra-individual consistency in fGC concentrations were demonstrated; fGCcv values demonstrated inter-individual variation but not intra-individual consistency.

- Table 4.17 summarises the significant effects observed in models describing the relationship between personality construct scores, stress and life-history variables.

Table 4.17: Summary of relationships between personality construct scores, stress and life-history variables. In parentheses by the variables, (+) and (-) indicate that the models predicted positive or negative associations between the scores and the variables or interactions.

Personality Construct	Sex Differences	♂	♀
Excitability	♂ > ♀	fGCcv (+)	None
Sociability	None	None	Rank*Age (+)
Tactility	♂ < ♀	fGCcv*Age Rank*Age	fGC (+) Age(-)
Confidence	None	None	Rank*Group (+)
Introversion	♂ > ♀	None	None
Boldness	None	None	None
Exploration	None	None	fGC*Group (+)

4.4 Discussion

4.4.1 Barbary Macaque Stress Physiology

In this study, individuals varied significantly in both their physiological stress levels (mean fGC concentrations) and physiological stress reactivity (fGCcv). For all individuals, including those with the highest variation in physiological stress levels, intra-individual consistency of physiological stress level was demonstrated over the study period. However, intra-individual consistency was not found for physiological stress reactivity. Therefore, individuals generally appear to have a consistent overall physiological stress profile, but reactivity may vary between seasons in order to cope with reproductive demands and climatic variation, which are known stressors for this species (Young et al, 2013; 2014a). Thus, in Barbary macaques, stress physiology may be tenuously considered a "state" in terms of the state-dependent hypothesis (Dall et al, 2004; section 4.1.2).

The finding of intra-individual consistency in physiological stress levels, or baselines, is interesting as most wild population studies report low to non-existent levels of intra-individual consistency over time and context in physiological stress levels (Cook et al, 2011; Baugh et al, 2014; Grace & Anderson, 2014; Sparkman et al, 2014; Montiglio et al, 2015; reviewed in Hau et al, 2016). It has been proposed that this inconsistency might be a consequence of the highly heterogeneic environment wild animals occupy in terms of climate, food availability and social interactions, which generates considerable variation in the experience of stressors between individuals (Romero et al, 2000; Hau et al, 2016). However, the aforementioned studies of intra-individual inconsistency in physiological stress levels were conducted in wild avian (Baugh et al, 2014; Grace & Anderson, 2014), fish (Cook et al, 2011), reptile (Sparkman et al, 2014) and rodent species (Montiglio et al 2015), which are potentially highly susceptible to environmental stressors such as climate or predation threat. Exploring why some wild-living organisms are capable of maintaining relatively stable glucocorticoid levels compared to other species may also reveal the capability of a species to cope with significant environmental changes, such as may be experienced due to global warming or other anthropogenically-induced factors (Hau et al, 2016).

Both stress physiology and life history variables were related to the expression of personality constructs. These relationships were specific to sex and, in some cases, to group membership for subjects. Significant differences in stress physiology were observed between the sexes and in some cases between groups. Females tended to have higher stress levels than males; males tended to have higher stress reactivity than females. Within sexes, Blue group subjects tended to have higher stress levels and reactivity than Green group subjects. For female primates, a number of studies have found a link between reproductive status and physiological stress levels, with peaks in cortisol during the peri-ovulatory phase and a nadir during mid-luteal phases (Ziegler et al, 1995; Saltzman et al, 1998), as well as elevated physiological stress levels during pregnancy (Ziegler et al, 1995; Pryce, 1996; Cavigelli, 1999; Hoffman et al, 2010). In the current study, all females, except two elderly adults, became pregnant during the mating seasons and this is likely to explain the sex differences in stress levels.

Data collection was conducted during and immediately after two breeding seasons, a period when males are aggressively competing and forming coalitions to gain access to females (Young et al, 2014b). Coalition formation is an adaptive behaviour of male Barbary macaques (Bissonnette et al, 2009, Berghänel et al, 2011; Young et al, 2014b) and effective coalitions may require endocrine flexibility to adjust swiftly between targeted aggression and social bonding. The "challenge hypothesis" posits that in order to meet competitive needs, testosterone expression will increase, causing an associated decrease in circulating cortisol (Wingfield et al, 1990). In male Barbary macaques, strong intra-sex social bonds attenuate environmentally-induced stress (Young et al, 2014a). Variable physiological stress reactivity may allow male Barbary macaques to rapidly modify behaviour in a dynamic social environment (Taff & Visoutek, 2016).

Group-level differences in physiological stress measures may be explained by differences in environment. The Blue group home range is dissected by a major road and contains two tourist sites and car parks (section 2.2; figure 2.2). Blue group subjects live in a highly-disturbed environment and frequently interact with tourists (personal observation). Human-macaque interactions are known to increase physiological stress and anxiety, and create health issues in this species (Maréchal et al, 2011, 2016; Borg et al, 2014). The Green group lives in a relatively undisturbed home range. Therefore, the high levels of, and greater within-individual variation in physiological stress observed in the Blue group is likely to reflect the differing levels of anthropogenic disturbance each group experiences.

4.4.2 Stress Physiology and Personality

Males had higher scores for Excitability than females, and in males, higher stress reactivity was associated with higher Excitability scores. Barbary macaque Excitability is a personality construct characterised by activity and high frequencies of short-term aggression and affiliation behaviours (chapter 3).

These behaviourally “excitable” and physiologically “reactive” individuals fit the generalised “Reactive” phenotype proposed by Koolhaas et al (1999). Such individuals have relatively high stress reactivity and tend to respond dynamically to aversive stimuli, either with aggression or by fleeing. Comparatively, “Proactive” individuals have low reactivity and tend to use strategies to avoid aversive stimuli (Koolhaas et al, 1999). This proactive profile is comparable to that of the female macaques in this study which had lower reactivity and lower Excitability scores. Barbary macaques live in female-bonded groups, therefore, male Barbary macaques live in a comparatively unstable social environment compared to females, and this instability appears to be reflected both in behavioural phenotype and stress physiology.

Results in relation to Excitability indicate that male and female Barbary macaques have very different relationships between physiological stress and the expression of personality. This was also apparent in the relationship found between Tactility scores and stress variables. For males, individuals with higher levels of stress reactivity had lower Tactility scores, and this trend was stronger in elderly adult males compared to adult males. The Tactility construct was characterised by high rates of allo- and self-grooming and has first been described in Barbary macaques (section 3.4). Allo-grooming is principally a positive social interaction (compared to “excitable” behaviours which are both pro- and anti-social, e.g. embraces and supplants respectively), while self-grooming may function as a displacement behaviour for elevated stress (Troisi, 2002). As previously described, for males, high stress reactivity was also associated with higher Excitability scores. Both allo- and self-grooming are sedentary behaviours and not easily compatible with “excitable” activity. Therefore, the high-reactivity, low-Tactility, high-Excitability relationship observed suggests the two personality constructs may represent two ends of one axis of personality which is linked to physiological stress reactivity. However, scores for Tactility and Excitability were not negatively correlated (section 3.4), so this explanation is not completely satisfactory. Previous work in primates found that higher HPA activation is associated with lower scores for personality types related to prosocial interactions (Byrne & Suomi, 2002; Capitanio et al, 2004) and the relationship between variation in stress reactivity and Tactility scores in male Barbary macaques found in this study appears to fit this trend. As with Excitability, exploring functional consequences of Tactility, such as social integration, may help to explain inter-individual variation in the expression of this personality construct among males.

Female stress reactivity was not related to Tactility scores, although higher stress levels were associated with higher Tactility scores when controlling for the effect of age (Tactility scores decreased with age in females). Previous work in female Barbary macaques found that giving grooming was associated with lower fGC levels (Shutt et al, 2007). A more recent study of both sexes found that allo-grooming was associated with elevated rates of anxiety (Semple et al, 2013), while a study of a semi-free ranging population of Barbary macaques found that the physiological stress effect of grooming was dependent on the nature of the relationship between female grooming partners (Sonnweber et al, 2015). In female chacma baboons (*Papio ursinus*), disruption to social networks or relationships elevate stress more in females than males (Cheney & Seyfarth, 2009). The positive relationship between Tactility scores and stress levels in female Barbary macaques may reflect a sex-specific physiological association to maintaining social relationships. Future personality research should examine non-female-bonded species to help identify whether the sex-dependent, stress-personality dynamics observed in this study are an artefact of social structure.

For females, a relationship was found between Exploration scores and the interaction between group and physiological stress levels. The Exploration construct was characterised by higher rates of visual inspection of the novel objects presented (section 3.4). Blue group females had higher Exploration scores than Green group females, and within each group, females with higher stress levels had higher Exploration scores. The group effect is probably explained by the level of human disturbance in the Blue group home range. The females of this group are known to interact with tourists and visit tourist sites where exploration of novel food items and objects can yield nutritional reward. This has potential conservation management implications if personality can be shaped by exposure to humans or human-disturbed environments (McDougall et al, 2006).

In humans, increased cortisol levels are associated with greater attention to perceived threats (Roelofs et al, 2007), and in non-human primates, emotional state predicts attention to social stimuli (Bethell et al, 2012). Under the proactive-reactive personality paradigm, higher HPA activity is associated with reactive behaviour and low active avoidance of stressors (Koolhaas et al, 1999). In the present study, the experimental assay for Exploration was designed to record responses to novel but non-threatening stimuli. The pattern of higher stress levels being associated with increased attentiveness to such stimuli may suggest that the stimuli were perceived as threatening, or alternatively, individuals with generally high physiological stress levels are inclined to be more vigilant and attentive to *any* stimulus, whether threatening or not. Male Exploration scores were not related to physiological stress. Montiglio et al (2012) assayed “exploration” in wild eastern chipmunks (*Tamias striatus*) by measuring the latency of subjects to explore novel environments rather than objects. Female chipmunk exploration scores were positively related to physiological stress levels, but this relationship was absent in males of the species. The emerging evidence is that exploration of novel environments or resources has a sex-dependent link to stress physiology.

As previously described, for male Barbary macaques, the nature of the association between Tactility scores and physiological stress reactivity varied dependent on different life stages which in turn may be associated with differing life history strategies. Although personality, stress reactivity and life history have been linked in wild chipmunks (Montiglio et al, 2015), the present study is the first time this has been demonstrated in wild primates. For elderly males, increases in stress reactivity were associated with lower Tactility scores than similar increases in stress variation in adult males. Physical deterioration and a potential shift in motivation from social integration to survival may explain the physiological associations of Tactility behaviours being more severe for elderly adults.

4.4.3 Life History and Personality

Within primatology, comparisons between age categories in personality expression are rare (Kendal et al, 2005). In humans, the expression of “active” personality constructs such as Neuroticism and Extraversion decrease with age, with individuals expressing socially sensitive personality constructs, such as Agreeableness and Conscientiousness, more in older age (Roberts et al, 2006). Humans and most primates, including Barbary macaques, have a “slow” pace-of-life, with heavy parental investment, at least in females, and an emphasis on survival in order to increase long-term fitness (Biro & Stamps, 2008). However, younger individuals face challenges related to social integration and assertion which may favour riskier behaviours (Fairbanks, 1993).

In the current study, elderly adult males had lower Excitability scores than adult males in the best fit model (although this relationship was non-significant in the second best fit model), which may be due to the physicality demands of “excitable” behaviours. For the Tactility construct, low-ranking elderly males had higher Tactility scores than the single high ranking elderly male, whereas in adult males, Tactility scores were lower in low ranking individuals. For elderly males, being of low rank, as well as less physically able to compete aggressively with younger individuals, higher Tactility scores may reflect a social strategy to increase tolerance within the group (Tiddi, 2011). In this way, low Excitability and high Tactility in certain older males could be similar to the increasingly “socially sensitive” personalities seen in older humans.

In females, the interaction between rank and age was related to lower Sociability scores with decreasing rank and increasing age. The finding related to age contrasts directly with the aforementioned predictions based on findings in humans or pace-of-life-based hypotheses. Low Sociability scores for elderly females may reflect a physical constraint, i.e. not being able to keep up with the group and remain central as it forages and travels. Both of the elderly females were no longer experiencing reproductive cycles (based on observations of anogenital swellings; Young et al, 2013) and neither gave birth to an infant during the study period. Sociability may be more beneficial to breeding females with immature offspring. Alternatively, infants are attractive to male and female Barbary macaques (Paul & Kuester, 1996); elderly females without infants may be unattractive social partners for other individuals within the group. The role of, and, in some species, the existence of, menopause in primates is uncertain and rarely observed in the wild (Paul et al, 1993; Walker & Herndon, 2008). These females both came from the Blue group, which is frequently provisioned by tourists. The nutritional benefits of human provisioning may have extended the lifespan of these two macaques and this once again hints at how human influence can shape the demographics of animal populations.

For females, a relationship was found between Confidence scores and the interaction between rank and group. However, the results of this particular model are difficult to interpret and confounded by the way the personality was quantified. Confidence as a construct was characterised by dominance, with individuals scoring highly if they were perceived to be dominant over conspecifics. For the Green group females, lower ranking individuals had higher Confidence scores, for the Blue group females, higher ranking individuals had higher Confidence scores. Behavioural data collection, used to quantify rank, occurred after questionnaire data collection, which was used to quantify Confidence (chapter 3). Therefore, rank and Confidence scores are not temporally linked. The Green group female hierarchy underwent significant upheaval, with the first- and second-highest-ranking females from the first mating season, ANN and JOA, deposed to become the first- and second-lowest-ranking females by the end of the study (table 4.8). The questionnaire ratings of ANN and JOA would have been completed when they were higher ranking. This finding highlights the caution required when trying to use different data sources which are not temporally linked to explain variation in personality. That said, there appears to be a link between Confidence and rank, which raises the issue to what degree rank position itself should be considered a personality phenotype (Neumann et al, 2013; Favati et al, 2014). Female Barbary macaques inherit ranks from their mothers, with typically little variation in rank position during their lifetime (Fooden, 2007), and this rank inheritance may explain the inheritance of certain personality traits which has been seen in some primate species (Fairbanks et al, 2004; Freeman et al, 2011; Brent et al, 2013a).

4.4.4 Conclusions and future directions

This study is the first to demonstrate relationships between personality, physiological stress and life history (sex, age and rank) in a wild primate. As such, it lends empirical data supporting the state-dependent hypothesis for the origin and maintenance of some personality constructs. It also demonstrates that although some aspects of personality may be stable within life history stage, other aspects of personality and its correlations with stress variables may change over the course of an individual's lifespan, as is known in humans but rarely demonstrated in animal models (Roberts et al, 2006).

Hormones do not act singularly, and future research in this field would benefit from simultaneous examination of multiple hormones, particular cortisol and testosterone, as has recently been done in humans (Kornienko et al, 2014). Future work could more accurately explore age-based variation in personality expression than was possible in this study. This project's cohort was predominantly adults (74%) and there were no males among the sub-adults (one sub-adult male started the study, but dispersed early in data collection). Personality research, by its nature, requires aggregating a lot of behavioural data, which limits the number of eventual data points available to include in statistical models. Consequently, multiple separate models had to be created for each personality whereas it would have been preferable to include all variables in one model for each research question. Examining many models inflates the potential of finding a significant result. However, without more subjects and thus more data points, it was impossible to include all personality scores in one model without overfitting the initial models. The statistical approach used in this study was a compromise based on sample size.

Personality, stress, life-history and their associations need to be studied from a functional perspective (Dingemanse & Réale, 2005). In the remaining chapter of this thesis, I will investigate how personality is related to social integration (chapter 5), a key predictor of survival in Barbary macaques (McFarland & Majolo, 2013; Lehmann et al, 2015).

5| Personality and Sociality in Wild Barbary Macaques

Abstract

For group-living animals, navigating the social environment is key to maximising the fitness benefits (e.g. detection of resources) and minimising the fitness costs (e.g. resource competition) of living in close proximity to conspecifics. The “social niche” hypothesis states that personality arises and is maintained when group-living individuals segregate into particular social niches and roles due to selective pressures and variation in fitness outcomes arising from the social environment. Relating personality expression to social relationships allows us to examine one process by which personality may arise and/or be maintained, as well as improving our understanding of how social cohesion can be achieved in social animals. Here, this study examines whether wild Barbary macaques are consistent in their social network positions, which would suggest a link between the consistency in behaviour, i.e. personality, and social outcomes. Then the personality expression of wild Barbary macaques is related to measures of social integration (centrality in social networks). Finally, the “social niche” hypothesis is examined by testing whether the subjects socially assorted themselves according to personality phenotype. Barbary macaques were consistent across time and contexts in their affiliative social network positions, but highly variable in their aggression social network positions. Personality was not a strong predictor of social network position: Exploration expression was positively associated with individual clustering coefficients in grooming networks, Excitability expression was positively associated with eigenvector centrality in nearest neighbour networks in females and negatively associated in males.

Personality homophily was found in nearest neighbour and co-feeding networks, providing empirical evidence supporting the "social-niche" hypothesis of personality.

5.1 Introduction

Most primate species are highly social (Smuts et al, 1987). Group-living is associated with a variety of benefits, such as reduced predation (Hamilton, 1971), enhanced detection of food sources (Gartlan & Struhsaker, 1972), access to mates (Swedell, 2012) and resilience to climatic variation (McFarland & Majolo, 2013). Sociality is not wholly beneficial and potential costs include exposure to disease and parasite transmission (MacIntosh et al, 2012) and increased competition for food or mating resources, which may also lead to agonistic interactions with associated detrimental physiological outcomes (Sapolsky, 1982; Abbot et al, 2003). In a number of primate species, empirical evidence suggests there is a net fitness benefit to maintaining social relationships (Silk, 2014). Among primate species investigated to date, the strength of an individual's social bonds is related to increased reproductive output (e.g. in chacma baboons [*Papio ursinus*; Silk et al, 2009], yellow baboons [*Papio cynocephalus*, Silk et al, 2003] and Assamese macaques [*Macaca assamensis*; Schülke et al 2010]), improved health (e.g. in humans [Fiori et al, 2006] and Japanese macaques [*Macaca fuscata*; Duboscq et al, 2016]) and survival (e.g. in Barbary macaques [McFarland & Majolo, 2013; Lehmann et al, 2015).

Inter-individual variation in the motivation and ability to form and maintain social bonds is expected to derive from inter-individual variation in certain characteristics. Among primate species, dominance rank (Range & Nöe, 2002; Seyfarth, 1976), and kinship (Silk et al, 2010) or a combination of these factors (Tinsley Johnson et al, 2014), are generally predictive of social relationships between individuals. Kinship-based bonds may develop due to established familiarity between individuals during development (Seyfarth et al, 2014). Rank may cause social segregation as low-ranking individuals avoid high-ranking individuals, particularly when there is competition for a particular resource (de Waal, 1991; Stahl & Kaumanns, 2003; Heesen et al, 2014). Alternatively, in social situations such as grooming, low-ranking individuals may proactively seek out higher-ranking individuals to groom in order to receive support and tolerance in other social situations (Seyfarth, 1977; Tiddi, 2011). Whether individuals from different ends of the dominance hierarchy affiliate may be determined by the degree of despotism in the social system of the species or population (Barret et al, 1999; Puga-Gonzalez, 2009). However, rank and/or kinship do not uniformly predict the number and strength of social relationships for individuals. Studies of chimpanzees (*Pan troglodytes*; Mitani, 2009), rhesus macaques (Massen & Sterck, 2013) and chacma and yellow baboons (Seyfarth et al, 2014) failed to find a direct relationship between measures of sociality and rank or kinship. Therefore, within behavioural ecology, there is a need to identify other factors that may motivate or influence patterns of social relationships both in primates and beyond this particular taxon.

Personality has only recently been suggested to explain inter-individual variation in social relationships (Krause, 2010). Research on personality suggests that individuals vary from one another not only in their typical behaviour but also in their degree of behavioural flexibility (Dingemanse & Wolf, 2010). Personality-based social relationships may develop through a process which is a combination of the apparent mechanisms involved in kinship- and rank-based social relationships. If individuals are behaviourally consistent rather than completely flexible, this reduces cognitive costs for social partners as individuals can be relied upon to behave in particular ways across time and contexts (Dall et al, 2004; Massen & Koski, 2014). In this way, personality may serve to accelerate familiarity between individuals (similar to kinship-based social bonding).

Individuals of a particular personality may not be compatible with other personality phenotypes, e.g. introverts may not be expected to form social relationships with extroverts or, alternatively, a process of "attraction to opposites" may occur. In humans, personality appears to influence the number and nature of social relationships (Selfhout et al, 2010). Extroverts tend to form a greater number of social relationships, while shyer individuals are more likely to report having close bonds with a limited number of social partners (Asendorpf & Wilpers, 1998).

Humans tend to show homophily based on personality (Klohnen et al, 2005; Selfhout et al, 2010), although Nelson et al (2011) reported empirical evidence that strong social ties can originate from an affinity to opposing personality phenotypes. Assortment by personality supports the "social-niche" hypothesis, which posits that individuals show consistent differences in behaviour due to specialisation for specific social roles, which are expected to be generated in relation to social challenges such as resource competition (Bergmüller & Taborsky, 2010). Interactions with conspecifics early in social development can affect the expression of behaviours linked with personality, such as aggression and boldness (Oliviera et al, 2001; Montiglio et al, 2013). Furthermore, in Gouldian finches (*Erythrura gouldiae*), a recent study found evidence of "social conformity" in personality expression, whereby finches appeared to express “bolder” behaviours in the presence of a bold individual and “shyer” behaviours in the presence of a shy individual (King et al, 2015). Social experience may influence the development and flexibility in personality expression for an individual, which in turn may affect social environment if this leads to assortment within a group based on particular traits (Croft et al, 2009). Results such as these suggest intra-individual consistency in behaviour may only be demonstrated when consistency in social structure permits. More work is required to understand the complex interplay between personality expression and social environment (Sih et al, 2015).

If personality is affected by and affects social environment, this can result in a complex feedback loop and fluctuating selection on personality traits (Aplin et al, 2013). The social-niche hypothesis predicts assortment based on personality homophily, i.e. if personality is shaped by the social niche an individual occupies, all other individuals within that niche will have similar personalities. However, negative-frequency selection on personality would result in greater social mixing between personality phenotypes (Dall et al, 2004). Whether a social-niche or negative-frequency mechanism is related to both social relationships and personality may depend on the social and ecological environment, both of which are likely to fluctuate in response to one another. Long-term, objective data on human social relationships are impractical to collect, therefore, investigating the role of personality in social relationships in animals is a promising avenue of research.

The association between personality and social relationships is well explored in avian and fish species. For example, “bold” great tits (*Parus major*) have greater numbers of social ties than “shy” individuals, but these shy individuals have stronger associations within their limited social relationships

(Aplin et al, 2013). The same pattern of associations based on boldness or shyness has also been shown in stickleback fish (*Gasterosteus aculeatus*; Pike et al, 2008). As with humans, there appears to be a trade-off between quantity and quality of relationships and tendencies to “choose” quantity or quality are related to personality. Personality homophily has also been found in other animal species: Trinidadian guppies (*Peocilia reticulata*) and great tits tend to shoal/flock with conspecifics of similar personality phenotype (Croft et al, 2009; Aplin et al, 2013). Studies on animals examining personality and sociality to date have largely focused on relatively simple social associations (proximity) and one bipolar axis of personality (shy/bold).

Social groups across the primate taxon are extremely diverse in terms of size, structure and nature (i.e. despotic or egalitatian), and involve a variety of complex social partnerships or relationships (e.g. coalitions, grooming partners etc; Smuts et al, 1987). Primates also appear to have highly complex personality structures (chapter 3), making them useful subjects for examining relationships between multi-faceted social and personality structures.

Given the expected complexity of the interactions between personality and sociality, it is advantageous for behavioural ecologists to consider social ties beyond dyadic assessments and to look at how personality shapes, and is shaped by, whole social environments using social network based approaches (Sih et al, 2009). While several studies have related personality to dyadic social bonds, the relationship between personality and social network measures is less well explored (Wilson et al, 2012). In primates, social network analysis (SNA) has been used to examine the relationships between network position and several fitness outcomes. In female rhesus macaques, the interaction between rank and proximity network position was associated with hormonal stress levels

(Brent et al, 2011). "Well connected" high-ranking females have lower faecal glucocorticoid levels than other females. In female Japanese macaques (*Macaca fuscata*), higher-ranking females are more central in grooming networks, and increased centrality is associated with higher parasitic burden (MacIntosh et al, 2012). In Barbary macaques, centrality in affiliative and aggression networks has been linked to survival during extreme climatic events (McFarland & Majolo, 2013; Lehmann et al, 2015). Furthermore, studies in humans and nonhuman primates have found evidence that social network positions are heritable (Fowler et al, 2009; Brent et al, 2013b).

It has been proposed that social phenotypes, as determined from SNA, are a component or reflection of personality phenotypes (Jacoby et al, 2014), yet, to date, few studies have been able to demonstrate consistent social phenotypes in a wild species and directly link these to personality assessments (Wilson et al, 2012; Aplin et al, 2015). This issue will be addressed directly in this study by exploring the relationship between personality and sociality in a behaviourally and socially complex primate species, the Barbary macaque.

5.1.1 Aims

Understanding the origin and maintenance of personality remains a focus of evolutionary ecology (Wolf & Weissing, 2010). As demonstrated, social integration appears to be a predictor of fitness outcomes in primates. Using SNA, this study examines whether personality predicts the degree of social integration for Barbary macaques, which may suggest personality has functional consequences and fitness-related outcomes in this species.

The main research question of this chapter is: "***What is the relationship between personality and sociality in wild Barbary macaques?"***

Personality, by definition, is correlated, consistent behaviour over time and context (Réale et al, 2007). Therefore, if any links between social network positions and personality phenotypes exist, we should expect subjects to occupy consistent social network positions over time and context (Aplin et al, 2015). This study will explore the social-niche hypothesis by examining the degree to which the study subjects socially assort themselves according to personality phenotypes (Aplin et al, 2013). Therefore, the three sub-questions of this chapter are:

Q1: ***Are individuals consistent in their social network positions? This would suggest a link between social network position and personality.***

Q2: ***Within social networks in which individuals consistently occupy similar network positions, does personality predict network position, particularly centrality and thus social integration?***

Q3: ***Within social networks in which individuals consistently occupy similar network positions, do individuals demonstrate homophily based on personality? This would provide support for the social niche hypothesis.***

5.2 Methods

5.2.1 Quantifying Personality Constructs

Full details on the methods used for quantifying personality are in Chapter 3. Seven personality constructs have been identified in Barbary macaques and each subject was assessed in the degree to which they expressed these constructs (represented by a "personality score"). For the purposes of the analyses in this chapter, for each subject (n=27), one mean score per personality construct was included from the total study period.

5.2.2 Constructing Social Networks

Behavioural data were collected using focal and scan sampling methodologies (Altmann, 1974). Details of methods for collecting behavioural data, including definitions of behaviours, are in chapter 2. Behavioural data were divided into three time blocks based on reproductive season and chronological order (table 2.7; chapter 2).

For each of the two groups and for each of the three time blocks, four social networks were constructed. Network position in affiliative and aggression networks has been predictive of survival in Barbary macaques (McFarland & Majolo, 2013; Lehmann et al, 2015). In this study, for each study group, three affiliation-type networks were studied (grooming, co-feeding and nearest neighbour) as well as one aggression network (includes contact and non-contact aggression). Co-feeding is a relatively unexplored network in wild primates (King et al, 2011); Barbary macaques live in a habitat with seasonal extremes in weather which can limit the availability of food resources (Majolo et al, 2013).

Therefore, the capacity to tolerate and be tolerated feeding alongside others is also likely to be key to survival.

Table 5.1 lists the behaviours and calculations used to construct networks. All networks were considered directed; in directed networks each edge (the interaction between subjects) has a direction (e.g. for grooming, an edge can represent grooming given or received by the node; Wasserman & Faust, 1994). Nearest neighbour and co-feeding networks do not involve directed interactions; however, if A's nearest neighbour is B, B's nearest neighbour is not always A (the same applies for co-feeding partners) and therefore, these networks should be analysed as directed (D. Farine, personal communication). All networks were weighted using the "simple ratio index" (SRI) which controls for the overall gregariousness of the individuals (Whitehead, 2008):

$$SRI = \frac{x}{x + y\mathrm{AB} + y\mathrm{A} + y\mathrm{B}}$$

Where:

x = observations of A and B performing interaction of interest (e.g. grooming, co-feeding, aggression or nearest neighbour)

yAB = observations where A and B are interacting an interaction not of interest (e.g. for grooming networks, duration of all interactions between A and B that are not grooming, such as co-feeding)

yA = observations where A is observed without B

yB = observations where B is observed without A

This calculation produces a value between 0 and 1, with 0 indicating the individuals were never seen associating and 1 indicating they were never observed apart.

Table 5.1: Composition of social networks analysed.

Network	Association	Calculation
Aggression	All contact (bites, slaps etc.) and non-contact aggression (chases, charges etc) between subjects	Frequency of aggression events A enacts to B per hour of observation time during focal sampling
Grooming	All dyadic grooming interactions between subjects	Proportion of total focal observation time A spent grooming or being groomed by B
Co-feeding	Feeding partnerships whereby two or more individuals sit within 5 metres of each other to feed on a shared food resource, e.g. within the same tree	Proportion of total focal observation time A spent co-feeding with B
Nearest neighbour	During hourly scans, a scan sample of the group was taken, recording which individuals were in proximity to each other. Nearest neighbour was recorded as the nearest other subject within 5m of the scan subject	Proportion of hourly group scans in which A was nearest neighbour to B

5.2.3 Calculating Social Network Metrics

Density was calculated for each generated network to examine overall network connectivity. Density is the ratio of observed edges to all possible edges within the network and thus provides a useful comparative measure of connectivity in different networks (Wasserman & Faust, 1994).

For each network, five different metrics were calculated for each subject (see table 2.11 for equations); these are the most common SNA metrics and have previously been linked to fitness outcomes in animal species (Croft et al, 2008; Wey et al, 2008; Farine & Whitehead, 2015):

In Strength & **Out Strength** – strength is the sum of all edge weights connected to the node; in a directed network these edges can be in or out of the node. A "tuning parameter", α, determines the relative importance of the number of edges a node has compared to the weights of these edges (Opsahl et al, 2010). In this study, for both in and out strength, $\alpha=1$, which means the sum of weights was used to calculate the strength values. Individuals with high strength interact frequently with other individuals. Strength was preferred to "degree" (the total number of connections an individual has) due to the relatively high densities of the networks in this study (table 5.2). The number and strength of connections may have negative fitness consequences as frequent interaction may increase risk of pathogen transfer from conspecifics (MacIntosh et al, 2012).

Betweenness centrality – a count of the number of shortest paths that flow through a node. Individuals with high betweenness are considered more central to the overall group network. In captive chimpanzees, the statistical simulations of the removal of individuals with high betweenness caused significant decreases in group cohesion (Kanigeisser et al, 2011). In the same species, individuals with high betweenness were more successful forming coalitions with conspecifics during aggressive encounters (Gilby et al, 2013).

Eigenvector centrality – measures both direct and indirect ties; individuals with high eigenvector centrality have strong associations with their interaction partners and these partners themselves have strong associations with their immediate partners within the network. In rhesus macaques, individuals with high eigenvector centrality have a strong influence on the timing and direction of group movements (Sueur & Petit, 2008). In the same species, eigenvector centrality has been shown to be a heritable trait (Brent et al, 2013b). In bottle-nosed dolphins (*Tursiops truncates*), eigenvector centrality is a predictor of survival (Stanton & Mann, 2012).

Individual clustering coefficient – calculated as the proportion of a given individual's social partners who are partners with each other, i.e. cliquishness. A high clustering coefficient suggests that an individual's neighbours interact frequently among themselves. In pig-tailed macaques (*Macaca nemestrina*), clustering coefficients increased following the removal of dominant individuals from the group (Flack et al, 2006). In chacma baboons, clustering coefficients increased in seasons with low food availability (Henzi et al, 2009). Clustering appears a conservative strategy in uncertain environments and could be directly linked to personality.

All SNA was conducted in R: In strength, out strength and betweenness were calculated using the *tnet* package (Opsahl, 2009), eigenvector centrality and individual clustering coefficient were calculated using the *igraph* package (Czardi & Nepusz, 2006).

5.2.4 Consistency of Social Network Positions

To test the intra-individual consistency in network metrics, the ANOVA-based measure of repeatability (R_A; chapter 2) was used. To test network type consistency, R_A within network type (grooming, co-feeding, nearest neighbour or aggression) for each group (Blue or Green) was examined. To test if individuals were consistent in network position, subjects were the factorial predictors of repeatability of each network metric. Subject consistency was examined across the three time blocks for each network type and each metric.

5.2.5 Examining Relationship between Personality and Social Network Position

For social networks where individuals demonstrated consistency in network position, a network covering the whole time period (i.e. not divided into three separate networks) was constructed. Metrics for subjects within these networks for the whole time period were then calculated. Social networks in which subjects were not consistent in social network position were no longer included in analyses going forward as the lack of consistency in network position was assumed to reflect a lack of association between personality and network position in these networks.

Linear models were constructed to examine whether personality scores were associated with social network metrics. One model per metric (five separate metrics) per personality (seven different personalities) per network (four network types) was required as the sample size was not sufficient to include all personality scores within one model (Burnham & Anderson, 2004; Bolker et al, 2009). Therefore, prior to analysis, Spearman's correlation coefficients were calculated for social network metrics within networks; if metrics were correlated, only one of these metrics would be examined in a model.

To further reduce the number of models examined, prior to the results of any model being considered two key steps were taken: comparison between full models and null models using log likelihood ratio tests, followed by a node permutation procedure to confirm the model result was significantly different from random as metrics for subjects are not independent of one another. This significantly reduced the number of final models to be considered.

Network metrics were standardised as z-scores (Yeo & Johnson, 2000) prior to analyses to enable subjects from both groups to be included in the same model (individuals in larger groups can have more ties and thus different values for the metrics considered here). For each model, a social network metric was the dependent variable, with personality score as a fixed factor, as well as sex, rank and age, which are known predictors of social bonding in primate species (Silk et al, 2009; Tinsley Johnson et al, 2014). Where relationships between personality scores and sex, rank or age were established in Barbary macaques (chapter 4), these interactions were included in the model. For these analyses, group was not included as a fixed factor as differences in personality scores between groups were not significant (unlike group-level differences in stress physiology in chapter 4). Collinearity of fixed factors was examined using variance inflation factors (VIF; Field et al, 2012). VIFs were calculated using the *car* package (Fox & Weisberg; 2011). For all models examined, no evidence of significant collinearity was observed (VIF ranged between 1.03 and 2.61 for all models; see table A9c in Appendix A9).

Full models were compared to a null model i.e. an intercept-only model, using likelihood ratio tests and considered significant when $p<0.05$ (Bolker et al, 2009). Model selection was not used in this chapter as in chapter 4 as the relationships between personality and sex, rank and age had already been established and could be incorporated into a full model. To examine the relationship between the dependent variable (network metric) and the fixed factors within the full models, Wald logistic regression tests were performed, with factors considered significant when $p<0.05$ (Bolker et al, 2009).

If full models were significantly different from null models *and* personality score was found to be a significant factor following Wald logistic regression tests, a node permutation procedure was performed on the network and associated model as social network metrics are not independent between individuals of the same group. Node permutations re-distribute attributes of nodes throughout the network while maintaining the same number of nodes (Farine & Whitehead, 2015). Thus, node permutations generate random networks (here, n=1000) and allow comparison between model outputs from the observed network and those from the randomised networks. Variables from these randomised networks were used in the full models described above (differing from null models and in which personality had a significant effect on the social network metric) and the resulting model coefficients compared to the observed network and model. If the observed model coefficient was greater than (or less than in the case of a negative coefficient) 95% of the randomised coefficients, the observed model was considered to be significantly different from random.

5.2.6 Determining Social Assortativity by Personality

For the assortment analyses (section 5.2.7), rather than focusing on individual personality constructs, hierarchical cluster analysis was performed to identify how personality constructs cluster. This was done to create an overall personality phenotype, which is preferable in an examination of homophily. For example, two individuals with similar Boldness scores, might have very different Sociability scores and would not occupy the same personality cluster, but if individuals occupy the same personality cluster, they express all personality constructs to a similar degree.

Scores for subjects for all personality constructs were standardised (z-scores; Yeo & Johnson, 2000) and subjected to hierarchical cluster analysis using the r package *pvclust* (Suzuki & Shimodaira, 2006). This uses multiscale bootstrap resampling to generate an "approximately unbiased" probability value (P-value) for a cluster; highly supported clusters have high P-values and clusters were accepted when P-values ranged between 0.95-1.00.

To determine whether associations within the network were related to personality, multiple regression quadratic assignment procedure (MRQAP) tests were conducted on the social networks. MRQAP tests are permutation tests for linear regression models of data organised in matrices (Krackhardt, 1988). The analysis examines relationships between a dependent matrix (the matrix of social associations in this case) and one or more independent matrices which characterise differences between nodes (e.g. age differences, genetic relatedness etc). These differences can be binary (for example 1 for same sex, 0 for different sex) or continuous (determined by the differences in values between the two nodes, for example differences in rank).

For these analyses, an overall social network for the whole time period was used where individuals had demonstrated consistency in network position in this type of network. Matrices of differences were calculated for personality (binary response of 1 for same or 0 for different personality cluster within a dyad), sex (binary response), rank (continuous variable, calculated by the difference in standardised rank [section 2.5]) and age (binary response whether in same age category, i.e. primiparous, adult or elderly adult). For each analysis, the test examined whether the associations within a network were related to differences in personality, sex, rank or age differences. Significance ($p<0.05$) was calculated based on the position of the observed slope estimate relative to the distribution of slopes from 1000 randomisations (Farine, 2013). As MRQAP considers the whole network and matrix structure, each group and network type had to be analysed separately.

Analyses were performed using *asnipe* package (Farine, 2013) in which permutations are conducted using a "double-semi-partialing" (MRQAP.DSP) procedure (Dekker et al, 2007). Consider we want to determine whether:

$X \approx Y + Z$; where, X is an association matrix and Y and Z are matrices of differences between nodes.

MRQAP.DSP randomises the residuals from the regression on each independent variable (Y and Z) in order to calculate the p-value (Farine, 2013).

5.3 Results

5.3.1 Social Networks, Metrics and Repeatability

Table 5.2 lists the densities for all networks across the three time periods.

Table 5.2: Densities for all networks across the three time periods.

Network	Density					
	Blue Group			Green Group		
	Timeblock					
	1	2	3	1	2	3
Aggression	0.55	0.24	0.56	0.48	0.13	0.31
Grooming	0.66	0.48	0.52	0.55	0.29	0.37
Co-feeding	0.83	0.61	0.52	0.80	0.52	0.52
Nearest neighbour	1	0.97	0.98	0.73	0.38	0.93

Consistency in network position for subjects was examined across the three time blocks. Subjects were consistent across time blocks in at least one network metric for grooming, co-feeding and nearest neighbour networks but not aggression networks (table 5.3). The Green group experienced a number of changes in both male and female dominance hierarchies during the study period (section 4.3.4). Therefore, the consistency of aggression network positions for each group were then analysed separately to see if the Green hierarchy changes explained the low levels of consistency in aggression network positions. However, both groups were highly inconsistent in aggression network positions: for the Blue group, R_A for network metrics of subjects ranged from -0.23 to 0.18; for the Green group, R_A for network metrics of subjects ranged from -0.37 to 0.07. Based on these findings, social networks for grooming, co-feeding and nearest neighbour were constructed for the whole study period (10/10/2013-18/04/2015). Aggression networks were no longer included in the analysis as the lack of network position consistency by subjects in these networks was assumed to reflect a lack of relationship between aggression network position and personality.

Densities of overall networks for grooming, co-feeding and nearest neighbour are listed in table 5.4. Networks for both groups appeared highly connected and dense, with average density of 0.89($\pm$0.14). These network densities are much higher than previously reported in Barbary (Lehmann et al, 2015) and other macaque species (e.g. rhesus macaques; Brent et al, 2013c). Figures 5.1 and 5.2 illustrate these networks for each group. For each of these networks, metrics for individuals were recalculated for subsequent analyses.

Table 5.3: Consistency across time blocks and confidence intervals for social network metrics of subjects. Significant results are in bold text.

Network	Metric	R_A	95 % confidence interval		*P*
Aggression	Out strength	-0.15	-0.33	0.04	0.87
	In strength	-0.08	0.10	-0.29	0.86
	Betweenness	-0.10	-0.30	0.10	0.81
	Eigenvector	-0.10	-0.31	0.10	0.81
	Clustering	-0.24	-0.39	-0.09	<0.99
Grooming	**Out strength**	**0.29**	**0.03**	**0.55**	**0.01**
	In strength	**0.36**	**0.11**	**0.62**	**<0.01**
	Betweenness	0.15	-0.10	0.41	0.10
	Eigenvector	**0.32**	**0.06**	**0.58**	**<0.01**
	Clustering	-0.23	-0.38	-0.07	0.99
Co-feeding	**Out strength**	**0.24**	**-0.02**	**0.50**	**0.02**
	In strength	**0.25**	**-0.01**	**0.51**	**0.02**
	Betweenness	**0.27**	**0.01**	**0.53**	**0.02**
	Eigenvector	**0.29**	**0.03**	**0.55**	**0.01**
	Clustering	0.17	-0.09	0.43	0.07
Nearest neighbour	Out strength	0.05	-0.19	0.29	0.29
	In strength	0.16	-0.10	0.42	0.08
	Betweenness	0.05	-0.19	0.29	0.27
	Eigenvector	**0.31**	**0.05**	**0.57**	**0.01**
	Clustering	-0.11	-0.31	0.10	0.92

Table 5.4: Social network densities for networks across full study period.

Network	Blue Group	Green Group
Grooming	0.74	0.69
Co-feeding	0.93	0.99
Nearest neighbour	1.00	1.00

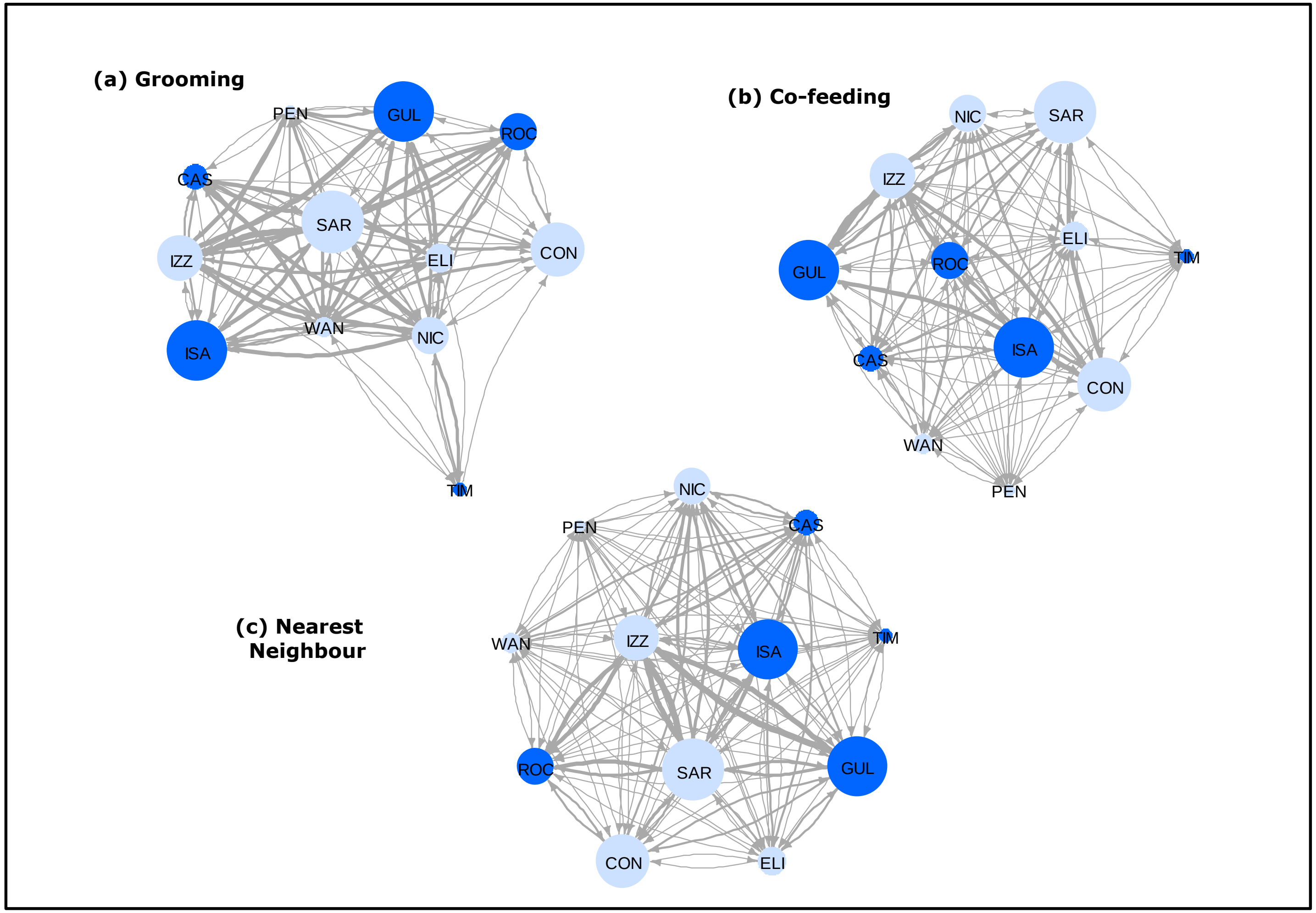


Figure 5.1: Social networks for the Blue group; (a) Grooming, (b) Co-feeding and (c) Nearest neighbour (n = 12 for all graphs). In each network, nodes are coloured to indicate sex (dark = male; light = female) and scaled based on rank (larger node = higher rank/more dominant). Edges between nodes are scaled according to the strength of the association.

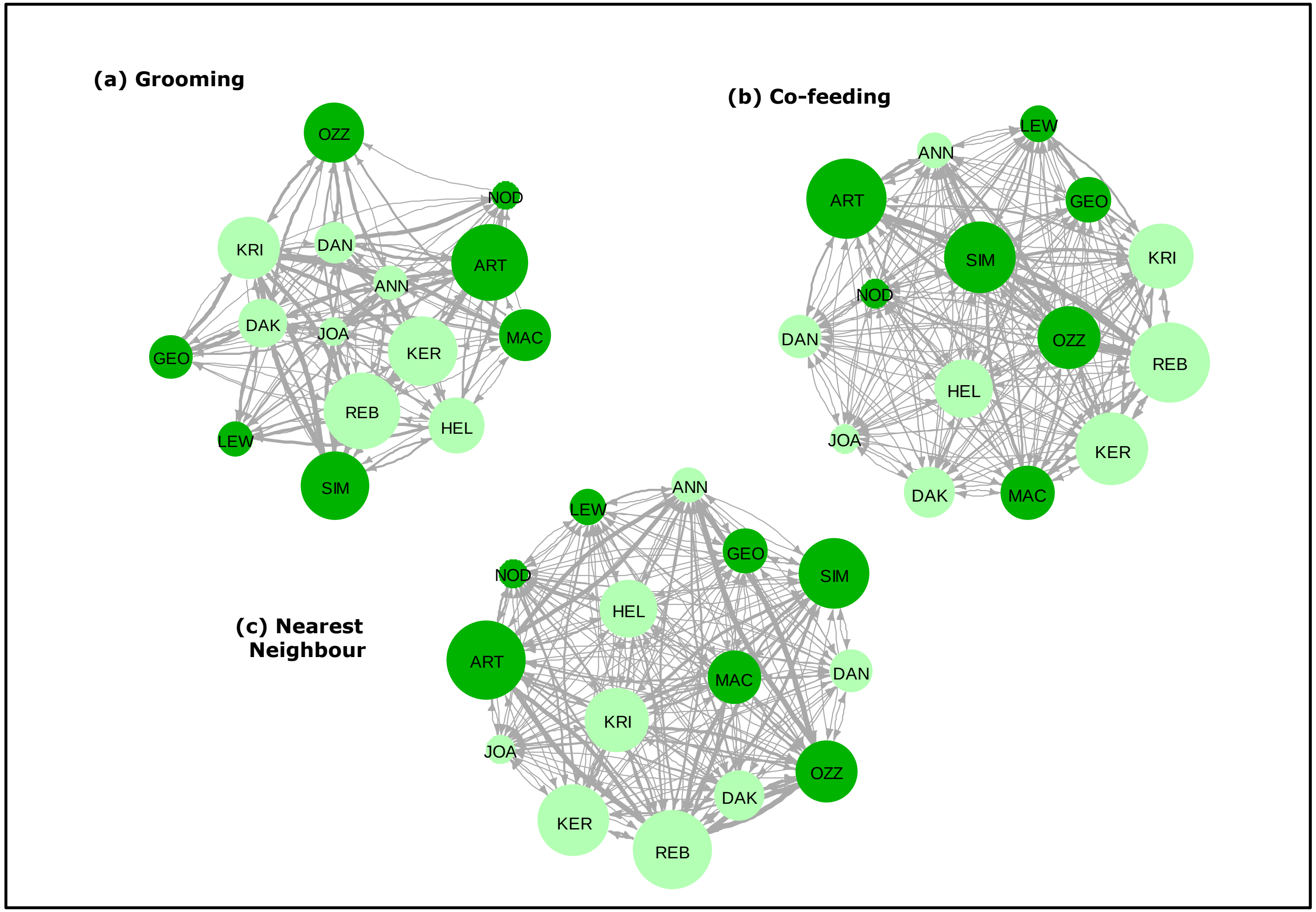


Figure 5.2: Social networks for the Green group; (a) Grooming, (b) Co-feeding and (c) Nearest neighbour (n = 15 for all graphs). In each network, nodes are coloured to indicate sex (dark = male; light = female) and scaled based on rank (larger node = higher rank/more dominant). Edges between nodes are scaled according to the strength of the association.

5.3.2 The Relationship between Personality and Social Network Position

Spearman's correlation coefficients were examined between the different networks metrics for each subject within one network type (n=27). For example, in the grooming network, the five network metrics of each subject were analysed for correlations within individuals.

Results are shown in table 5.5. **Eigenvector centrality** was highly positively correlated (r_s ranged between 0.54-0.98) with all other network metrics with the exception of **individual clustering coefficient**. Eigenvector centrality and individual clustering coefficient were negatively correlated in grooming and co-feeding networks. Therefore, models focused on whether personality score was associated with either eigenvector centrality or individual clustering coefficient.

Spearman's correlations were then calculated between subject metrics in different network types, focusing on eigenvector centrality and individual clustering coefficient, to see how correlated overall network structures were. Table 5.6 presents the results; **eigenvector centrality** values for subjects were correlated between **nearest neighbour** and **co-feeding networks** (r_s = 0.88; $p<0.01$; n=27), between **grooming** and **nearest neighbour** (r_s = 0.44; p=0.02; n=27), but not between grooming and co-feeding networks (r_s = 0.25; p=0.07; n=27). Individual clustering coefficients for subjects in the three networks did not correlate (r_s ranged between -0.24 and 0.25). As some of the metrics were not correlated across all network types, models were constructed for metrics from all of these networks.

Table 5.5: Spearman's correlation coefficients between network metrics for subjects within network types (n=27 for all correlations). Statistically significant correlations are in bold (p<0.05).

Network	Metric	In strength	Betweenness	Eigenvector centrality	Individual clustering coefficient
		r_s	r_s	r_s	r_s
Grooming	Out strength	0.15	**0.64**	**0.80**	**-0.61**
	In strength		**0.55**	**0.62**	-0.30
	Betweenness			**0.79**	**-0.44**
	Eigenvector				**-0.46**
Co-feeding	Out strength	**0.86**	**0.52**	**0.54**	-0.35
	In strength		**0.55**	**0.63**	-0.29
	Betweenness			**0.83**	**-0.46**
	Eigenvector				-0.41
Nearest neighbour	Out strength	**0.98**	**0.73**	**0.98**	0.27
	In strength		**0.76**	**0.97**	0.26
	Betweenness			**0.72**	0.14
	Eigenvector				0.11

Table 5.6: Spearman's correlation coefficients between eigenvector centrality and individual clustering coefficient for each subject across network types (n=27 for all correlations). This was done to examine correlations in overall network structure between different network types. Statistically significant correlations are in bold (p<0.05).

Metric	Network	Co-feeding	Nearest neighbour
		r_s	r_s
Eigenvector centrality	Grooming	0.25	**0.44**
	Co-feeding		**0.88**
Individual clustering coefficient	Grooming	-0.24	0.25
	Co-feeding		-0.11

For the nearest neighbour network, there was no variation between individuals in individual clustering coefficient, therefore, analysing a model including this network and metric was not possible. VIF analysis revealed low levels of collinearity between fixed factors (personality, sex, rank and age) in the full models (VIF mean 1.43[±0.67]; see table A9c in Appendix A9 for all VIF results).

Table 5.7 shows the log likelihood ratio results comparing full models to null models. Full models examined the relationship between social network metrics (eigenvector centrality or individuals clustering coefficient) and personality construct scores (as well as sex, rank and age) to null models (intercept only).

Full models which differed significantly from null models were then subjected to Wald logistic regression analyses to see if personality score was associated with social network metrics (see tables A10e-A10i in Appendix A10 for the results of these regression analyses). Models where personality scores were associated with social network metric were subjected to node permutation analysis to see if the association between personality and social network metric was greater (or less in the case of a negative coefficient) than expected by chance. Table 5.8 describes how coefficients from full models for the effect of personality scores in the observed networks differed from those of the randomised networks. As the research question focused on the effect of personality on network position, here comparisons of observed to random model coefficients focused only on the coefficient of personality scores within the model, i.e. one coefficient (for personality) per random model was being compared to one coefficient (for personality) from the observed models.

Table 5.7: Results of likelihood ratio tests, comparing full to null models when examining the relationship between personality scores, sex, rank, age and social network metrics (all full models detailed in tables A10e-A10i in Appendix 10). Only full models with significant differences to null models (indicated here by bold text) were subjected to regression and node permutation analyses.

Network	Metric	Personality in model	F	df	*P*
Grooming	Eigenvector	**Excitability**	**5.67**	**6**	**<0.01**
		Sociability	**5.76**	**6**	**<0.01**
		Tactility	**5.57**	**7**	**<0.01**
		Confidence	**8.27**	**6**	**<0.01**
		Introversion	**10.56**	**5**	**<0.01**
		Boldness	**9.16**	**4**	**<0.01**
		Exploration	**8.51**	**4**	**<0.01**
Grooming	Clustering	Excitability	2.24	6	0.08
		Sociability	1.43	6	0.25
		Tactility	1.26	7	0.32
		Confidence	1.92	6	0.13
		Introversion	9.26	5	0.08
		Boldness	2.24	4	0.10
		Exploration	**3.22**	**4**	**0.03**
Co-feeding	Eigenvector	**Excitability**	**5.18**	**6**	**<0.01**
		Sociability	**12.02**	**6**	**<0.01**
		Tactility	**5.32**	**7**	**<0.01**
		Confidence	**4.32**	**6**	**0.01**
		Introversion	**10.32**	**5**	**<0.01**
		Boldness	**6.24**	**4**	**<0.01**
		Exploration	**6.00**	**4**	**<0.01**
Co-feeding	Clustering	Excitability	0.99	6	0.46
		Sociability	**3.43**	**6**	**0.03**
		Tactility	1.62	7	0.19
		Confidence	1.54	6	0.21
		Introversion	1.33	5	0.29
		Boldness	1.57	4	0.22
		Exploration	1.35	4	0.28
Nearest neighbour	Eigenvector	**Excitability**	**5.09**	**6**	**<0.01**
		Sociability	**11.70**	**6**	**<0.01**
		Tactility	**3.88**	**7**	**0.01**
		Confidence	**3.51**	**6**	**0.02**
		Introversion	**8.55**	**5**	**<0.01**
		Boldness	**4.49**	**4**	**0.01**
		Exploration	**4.12**	**4**	**0.01**

Table 5.8: Permutation results comparing personality score coefficients from models based on observed networks in which personality score was significantly associated with network metric, to coefficients of models based on randomised networks; only models with coefficients different from random models (in bold text) are subsequently reported (tables 5.9 and 5.10).

Network	Metric	Personality	Proportion observed β < randomised β	Proportion observed β > randomised β
Grooming	Eigenvector	Excitability	0.53	0.47
		Sociability	0.45	0.55
		Tactility	0.41	0.59
		Confidence	0.11	0.89
		Introversion	0.38	0.62
		Boldness	0.24	0.76
		Exploration	0.70	0.30
Grooming	Clustering	**Exploration**	**0.04**	**0.96**
Co-feeding	Eigenvector	Excitability	0.75	0.25
		Sociability	0.58	0.42
		Tactility	0.22	0.88
		Confidence	0.58	0.42
		Introversion	0.81	0.19
		Boldness	0.32	0.68
		Exploration	0.48	0.52
Co-feeding	Clustering	Sociability	0.72	0.28
Nearest neighbour	Eigenvector	**Excitability**	**>0.95**	**<0.05**
		Sociability	0.20	0.80
		Tactility	0.24	0.76
		Confidence	0.33	0.67
		Introversion	0.57	0.43
		Boldness	0.24	0.76
		Exploration	0.70	0.30

Two full models differed significantly from null models and generated personality score coefficients within the observed networks which differed from the coefficients of randomised models. The first of these models (table 5.9) found that Exploration scores were positively associated with individual clustering coefficients in grooming networks (figure 5.3). This model also found a relationship between individual clustering coefficient and age, with older individuals tending to have higher clustering coefficients (figure 5.4). The second model (table 5.10) found that the interaction between sex and Excitability scores was associated with eigenvector centrality in nearest neighbour networks: for females, higher Excitability scores were associated with higher centrality, for males the inverse relationship was observed (figure 5.5). This model also found that higher ranking individuals tended to have higher centrality compared to low ranking individuals (figure 5.6).

Table 5.9: Results of full model exploring relationship between individual clustering coefficients and Exploration scores in the grooming networks of both groups. Significant effects are in bold.

	β	SE	Wald	*p*
Intercept	-1.82	1.09		
Exploration	**1.29**	**0.70**	**4.46**	**0.04**
Sex	-0.29	0.35	2.60	0.12
Rank	-0.17	0.18	0.34	0.57
Age	**0.77**	**0.33**	**5.48**	**0.03**

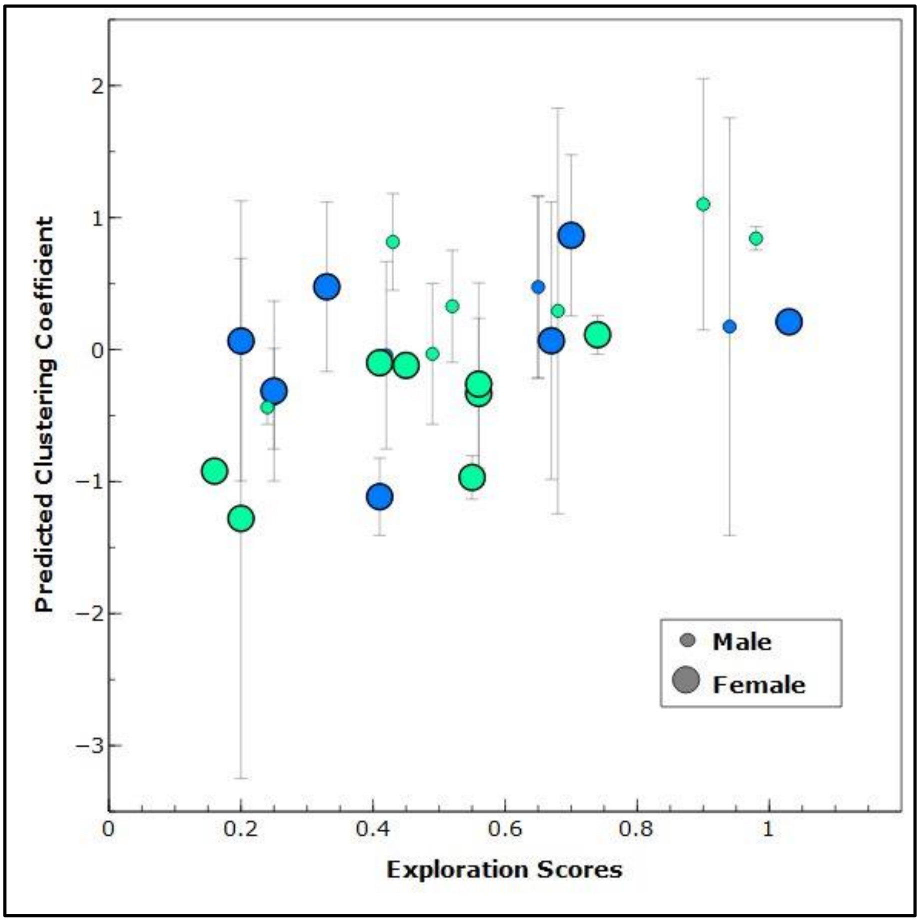


Figure 5.3: Plot of the predicted relationship between Explorations scores and individual clustering coefficients in grooming networks based on the model described in table 5.8 (n=27). Error bars represent residual values. All plots (n=27) are sized according to sex (see inset) and coloured to indicate group:

🔵 for Blue group; 🟢 for Green group

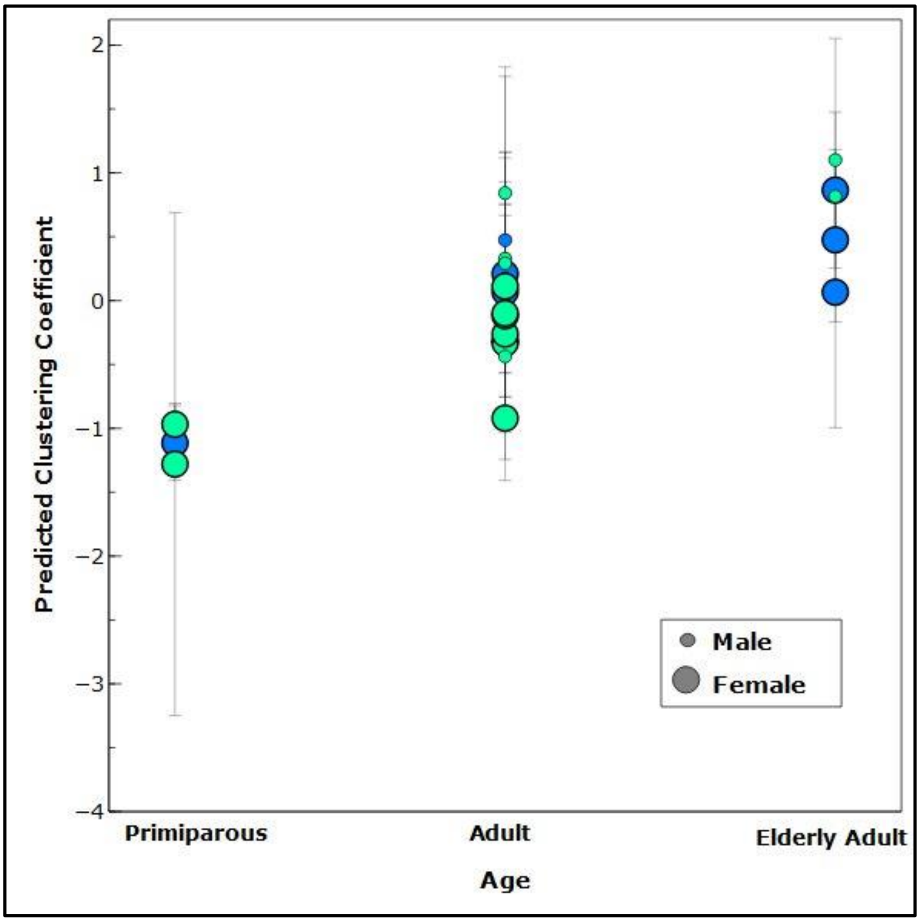


Figure 5.4: Plot of the predicted relationship between age categories and individual clustering coefficients in grooming networks based on the model described in table 5.8 (n=27). Error bars represent residual values. All plots (n=27) are sized according to sex (see inset) and coloured to indicate group:

● for Blue group; ● for Green group

Table 5.10: Results of full model exploring relationship between eigenvector centrality and Excitability scores in the nearest neighbour networks of both groups. Significant effects are in bold.

	β	SE	Wald	*p*
Intercept	3.97	1.95		
Excitability	-0.67	0.30	0.56	0.46
Sex	-1.95	0.89	1.37	0.26
Rank	**-0.64**	**0.17**	**18.98**	**<0.01**
Age	-0.41	0.50	0.12	0.73
Excitability*Sex	**0.41**	**0.14**	**9.25**	**0.01**
Excitability*Age	-0.06	0.12	0.23	0.64

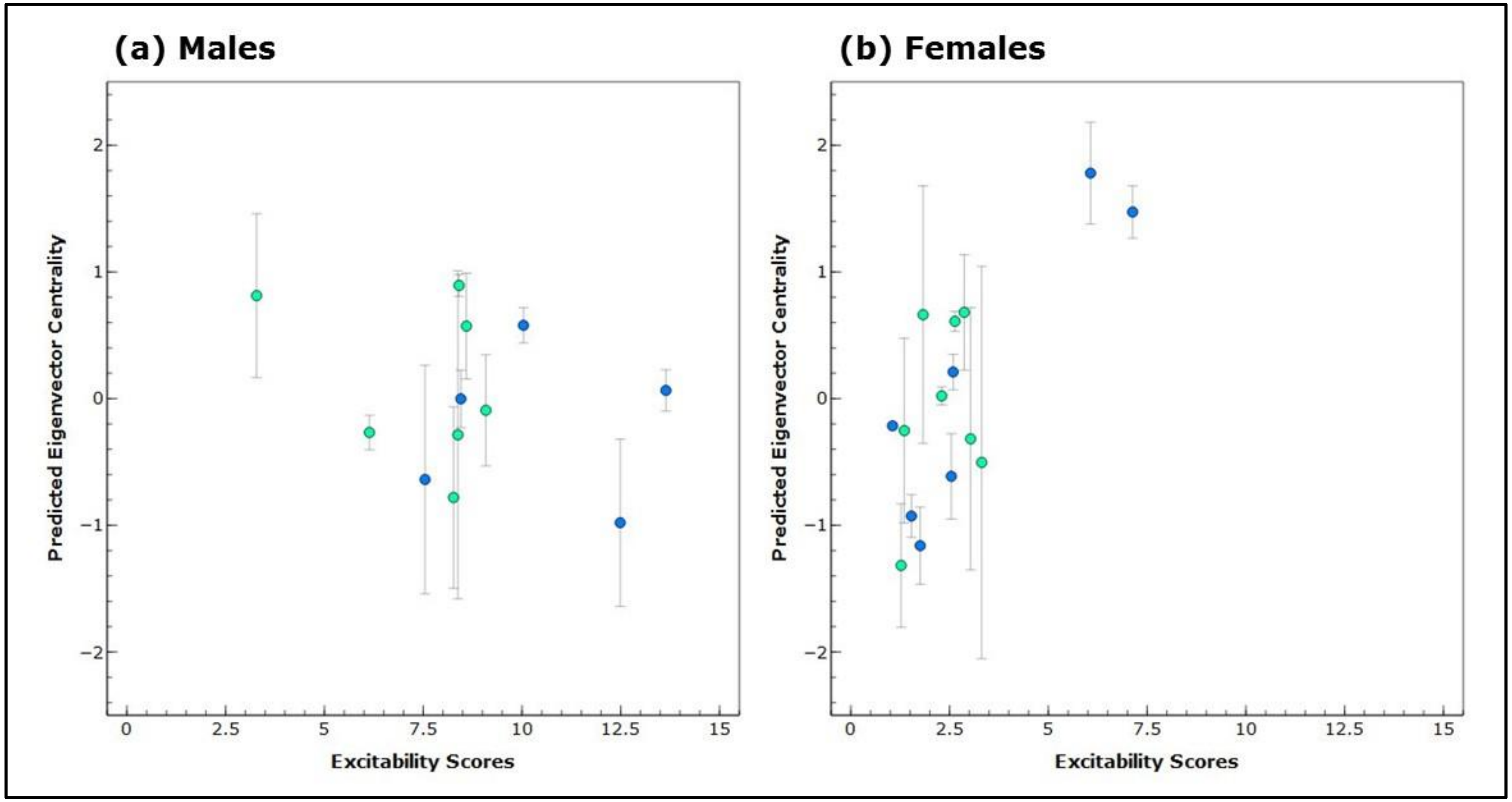


Figure 5.5: Plot of the predicted relationship between the interaction between sex and Excitability scores and eigenvector centrality in nearest neighbour networks based on the model described in table 5.10. Error bars represent residual values. Plots (n=27) are coloured to indicate group:

● for Blue group; ● for Green group

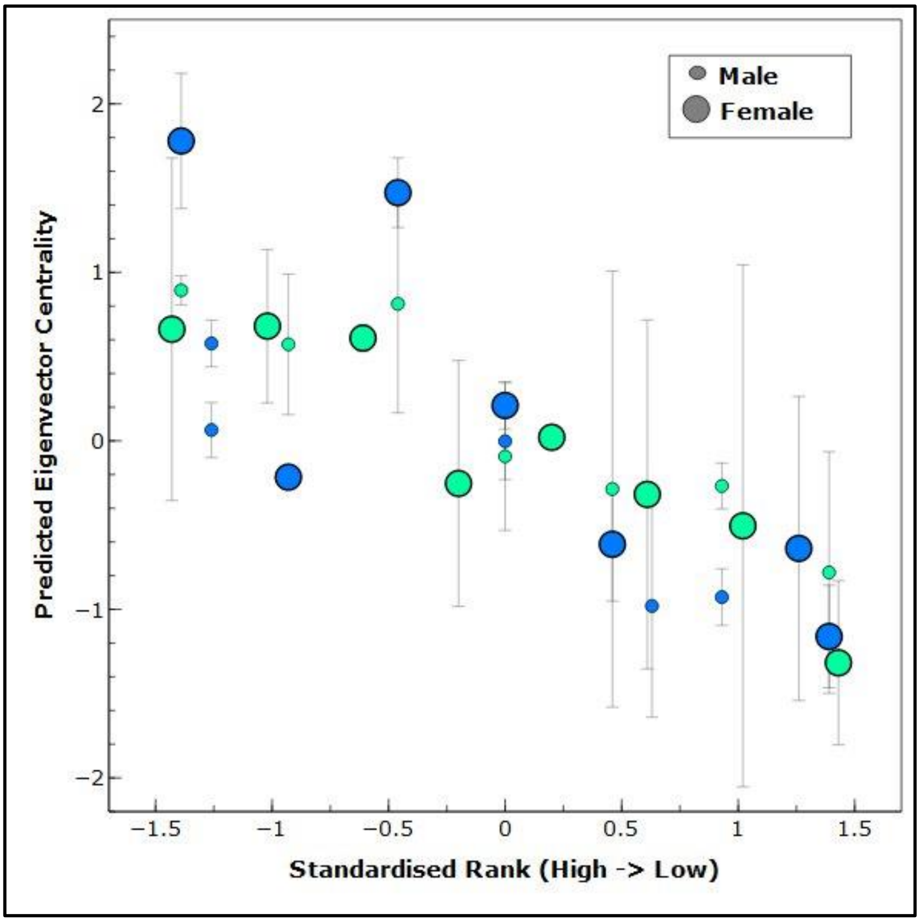


Figure 5.6: Plot of the predicted relationship between rank and eigenvector centrality in nearest neighbour networks based on the model described in table 5.10. Error bars represent residual values. Plots (n=27) are sized according to sex (see inset) and coloured to indicate group:

● for Blue group; ● for Green group

5.3.4 Assortment by Personality in Social Networks

Hierarchical cluster analysis of personality scores revealed three highly supported clusters (table 5.11; figure 5.7). Cluster 1 contained individuals (n=4) with generally low scores for Excitability, Sociability and Boldness, and high scores for Introversion. This cluster was termed "Unexcitable-Unsocial-

Introversion”. Cluster 2 contained individuals (n=10) with generally low scores for Excitability and Introversion, and generally high scores for Tactility. This cluster was termed “Unexcitable-Tactile-Extraversion”. In cluster 3, all individuals (n=13) tended to have higher than average Excitability scores and generally low Tactility. Therefore, this cluster was termed “Excitable-Non-Tactility”. Figure 5.8 illustrates each of the clusters.

Table 5.11: Results of hierarchical cluster analysis; three clusters were highly supported.

Cluster	Adjusted unbiased P-value	Standard error
(1) Inactive-Unsocial-Introversion	0.96	0.01
(2) Unexcitable-Tactile-Extraversion	0.97	0.01
(3) Excitable-Non-Tactility	0.97	0.01

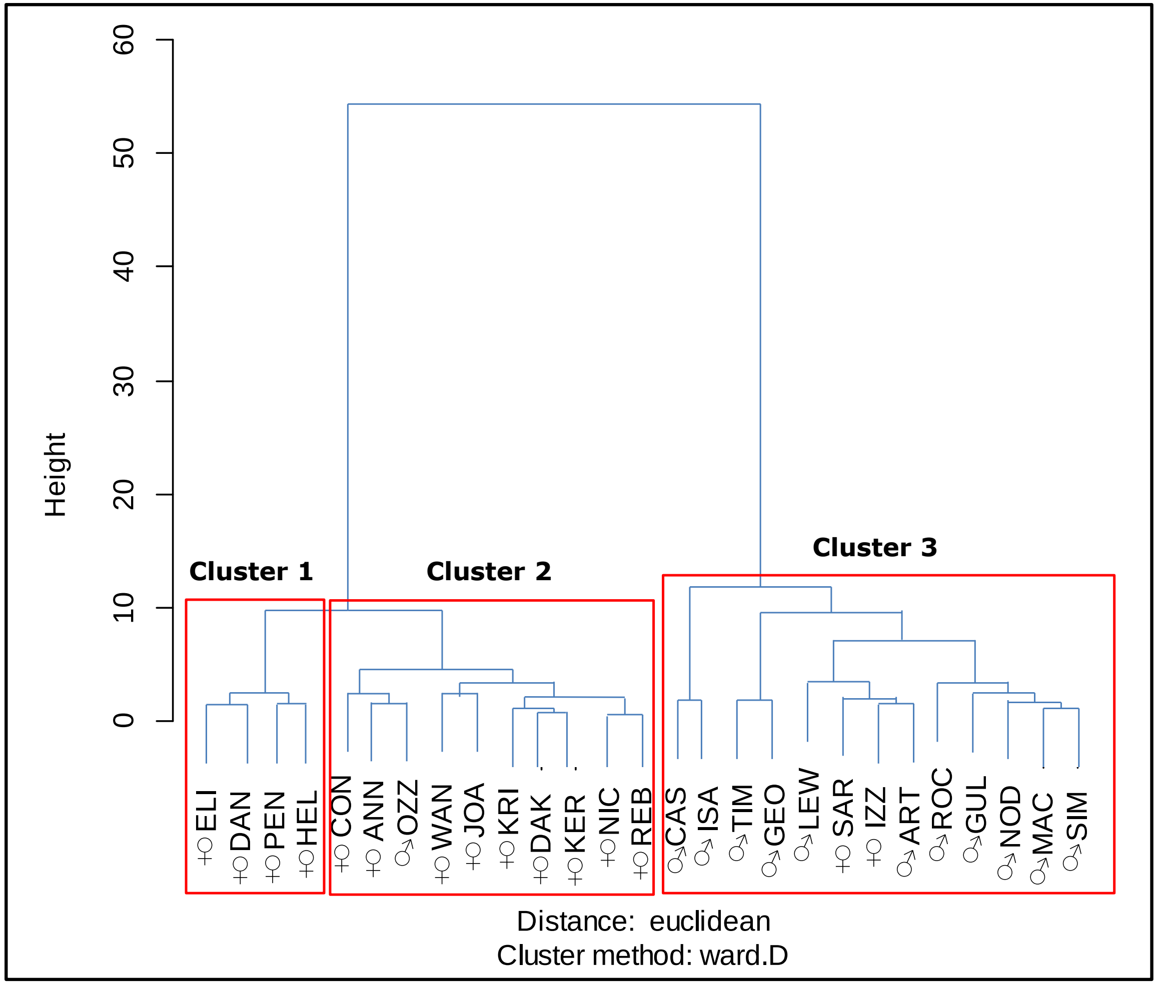


Figure 5.7: Dendrogram illustrating results of hierarchical clustering analysis (table 5.11). Highly supported clusters (P-values between 0.95-1.00) are highlighted in red boxes. The name of the individuals in the clusters are listed along the x-axis with symbols to indicate their sex.

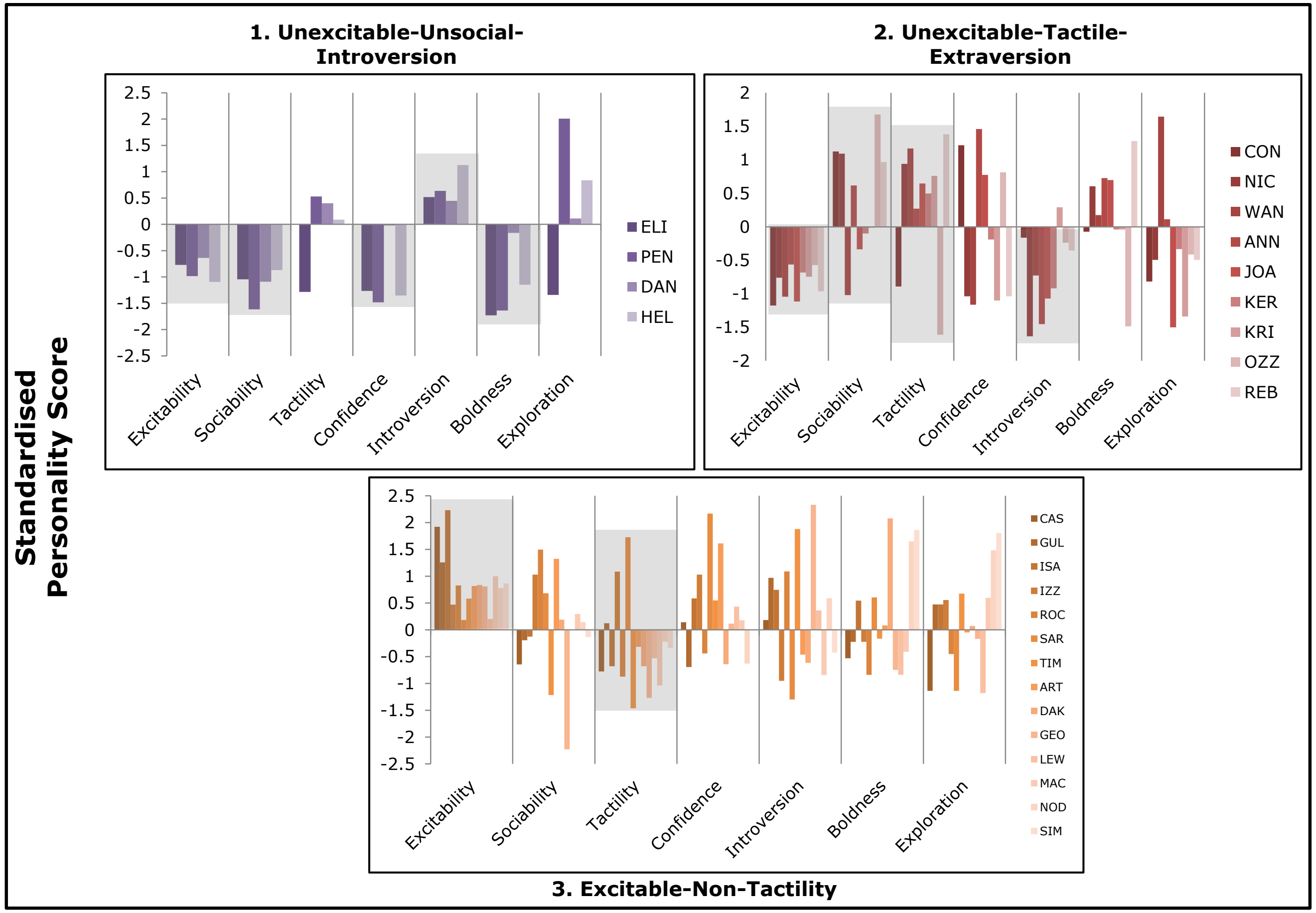


Figure 5.8: Personality clusters of Barbary macaques; each of the three bar charts represents a cluster. Each bar represents an individual and their standardised score for a particular personality indicated at the bottom of the chart. Patterns for similar scores within these clusters are highlighted by shaded grey boxes. (n = 27 for all clusters; n = 4 for cluster 1, n = 10 for cluster 2, and n = 13 for cluster 3).

To examine whether clusters were manifests of demographic characteristics, a linear model was created with cluster as the dependent variable and sex, rank, age and group as fixed factors. Wald logistic regressions were performed on fixed factors to see if they were associated with any clusters. Table 5.12 lists the results; cluster membership was related to sex: all individuals in cluster 1 were female and all but one male was in cluster 3.

Excitability was a defining personality in all three clusters and sex differences were found in the degree that males and females scored for this personality (chapter 4). As Excitability was a defining personality for all personality clusters, MRQAP analysis was conducted examining whether differences in Excitability scores (calculated as a continuous variable) predicted the distributions of associations within networks.

Table 5.12: Results of linear model exploring relationship between cluster membership and other demographic characteristics. Significant effects are in bold.

	β	SE	Wald	*p*
Model: Cluster ~ sex + rank + age + group				
Intercept	4.80	0.62		
Sex	**-1.09**	**0.22**	**22.97**	**<0.01**
Rank	-0.11	0.11	1.81	0.19
Age	-0.36	0.20	3.14	0.09
Group	-0.20	0.21	0.90	0.35

Evidence was found that subjects tended to associate with other individuals of the same personality cluster in certain social networks. MRQAP analysis examined whether dyads within the same personality cluster (as well as sex, age or rank) had stronger associations. As MRQAP uses individual matrices in its analysis, the two groups of macaques were considered separately.

Table 5.13 lists MRQAP results for the Blue group, table 5.14 for the Green group. Figures 5.9, 5.10 and 5.11 illustrate patterns of associations within the Blue group grooming, co-feeding and nearest neighbour networks respectively. Figures 5.12, 5.13 and 5.14 illustrate the patterns of associations within the Green group grooming, co-feeding and nearest neighbour networks.

For both groups, individuals tended to assort according to personality in the co-feeding (figures 5.10b and 5.13b) and nearest neighbour networks (figure 5.11b and 5.14b), but not within grooming networks (figures 5.9b and 5.12b). For both groups, across all networks, results suggested subjects also tended to assort themselves by sex, demonstrating preference for the opposite sex (figures 5.9c, 5.10c, 5.11c, 5.12c, 5.13c and 5.14c). In the Blue group co-feeding and nearest neighbour networks, evidence was found for rank homophily (figures 5.13d and 5.14d). In the Blue group grooming and nearest neighbour networks, evidence was found for age homophily (figures 5.12e and 5.14e).

Table 5.13: MRQAP results analysing the associations between dyads of the Blue group in (a) Grooming, (b) Co-feeding and (c) Nearest neighbour networks. "Difference in …" refers to whether dyads were in the same *personality* cluster, *sex* or *age* category (all binary), or *rank* (continuous calculated as difference in standardised rank). Coefficients from the regression analyses are reported, as well as the permutation results. Significant relationships are in bold text.

(a) Grooming

Variable	*B*	Proportion observed β > randomised β	Proportion observed β < randomised β	P-value
Intercept	0.27	1.00	0.00	0.00
Difference in Personality	0.02	0.66	0.34	0.72
Difference in Sex	**-0.11**	**<0.01**	**>0.99**	**0.03**
Difference in Rank	-0.02	0.23	0.77	0.45
Difference in Age	**0.02**	**0.98**	**0.03**	**0.04**

(b) Co-feeding

Variable	*B*	Proportion observed β > randomised β	Proportion observed β < randomised β	P-value
Intercept	0.01	1.00	0.00	0.00
Difference in Personality	**<0.01**	**0.99**	**0.01**	**0.01**
Difference in Sex	**-0.02**	**<0.01**	**>0.99**	**0.00**
Difference in Rank	**-0.02**	**<0.01**	**>0.99**	**0.01**
Difference in Age	<0.01	0.94	0.06	0.12

(c) Nearest neighbour

Variable	*B*	Proportion observed β > randomised β	Proportion observed β < randomised β	P-value
Intercept	0.11	1.00	0.00	0.00
Difference in Personality	**0.05**	**1.00**	**0.00**	**0.00**
Difference in Sex	**-0.04**	**0.00**	**1.00**	**0.00**
Difference in Rank	**-0.02**	**0.00**	**1.00**	**0.00**
Difference in Age	0.03	0.98	0.00	0.03

Table 5.14: MRQAP results analysing the associations between dyads of the Green group in (a) Grooming, (b) Co-feeding and (c) Nearest neighbour networks. "Difference in …" refers to whether dyads were in the same *personality* cluster, *sex* or *age* category (all binary), or *rank* (continuous calculated as difference in standardised rank). Coefficients from the regression analyses are reported, as well as the permutation results. Significant relationships are in bold.

(a) Grooming

Variable	*B*	Proportion observed β > randomised β	Proportion observed β < randomised β	P-value
Intercept	0.25	1.00	0.00	0.00
Difference in Personality	0.02	0.73	0.27	0.53
Difference in Sex	**-0.12**	**0.00**	**1.00**	**0.00**
Difference in Rank	-0.01	0.36	0.64	0.75
Difference in Age	-0.02	0.26	0.74	0.51

(b) Co-feeding

Variable	*B*	Proportion observed β > randomised β	Proportion observed β < randomised β	P-value
Intercept	0.01	1.00	0.00	0.00
Difference in Personality	**<0.01**	**1.00**	**0.00**	**0.00**
Difference in Sex	**-0.01**	**0.00**	**1.00**	**0.00**
Difference in Rank	<0.01	0.50	0.50	0.97
Difference in Age	<-0.01	0.06	0.94	0.10

(c) Nearest neighbour

Variable	*B*	Proportion observed β > randomised β	Proportion observed β < randomised β	P-value
Intercept	0.10	1.00	0.00	0.00
Difference in Personality	**0.04**	**1.00**	**0.00**	**0.00**
Difference in Sex	**-0.05**	**0.00**	**1.00**	**0.00**
Difference in Rank	<0.01	0.59	0.41	0.80
Difference in Age	-0.01	0.04	0.96	0.08

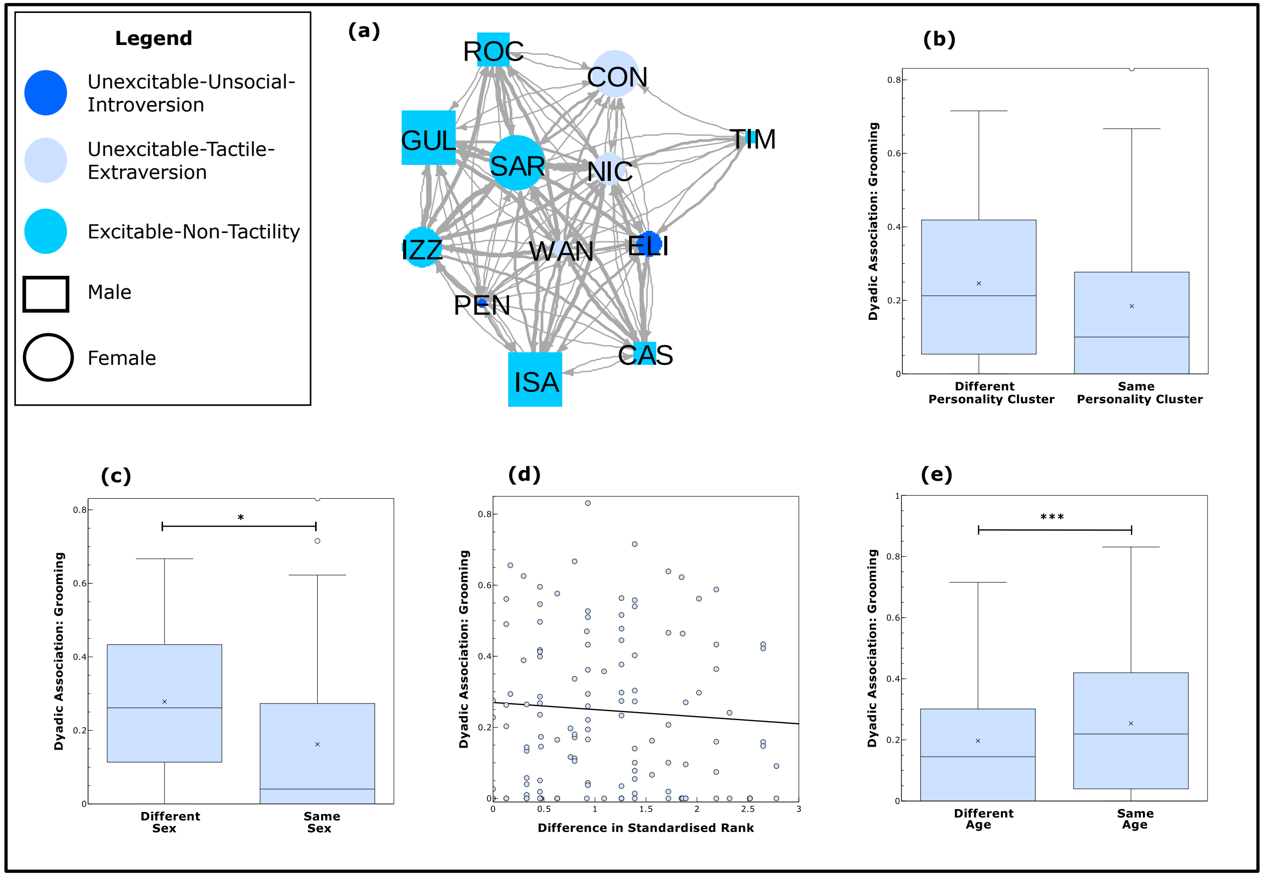


Figure 5.9: Patterns of homo- and heterophily in the Blue group grooming network. In the network graph (a), nodes are coloured according to personality cluster, shaped according to sex (see legend inset) and sized according to rank (increasing size corresponding with higher rank) (n = 12). The inset graphs (b), (c), (d) and (e) illustrate relationships between dyadic grooming associations (proportion of time dyads groomed relative to overall observation time) and differences in personality cluster, sex, rank and age respectively (n=132).

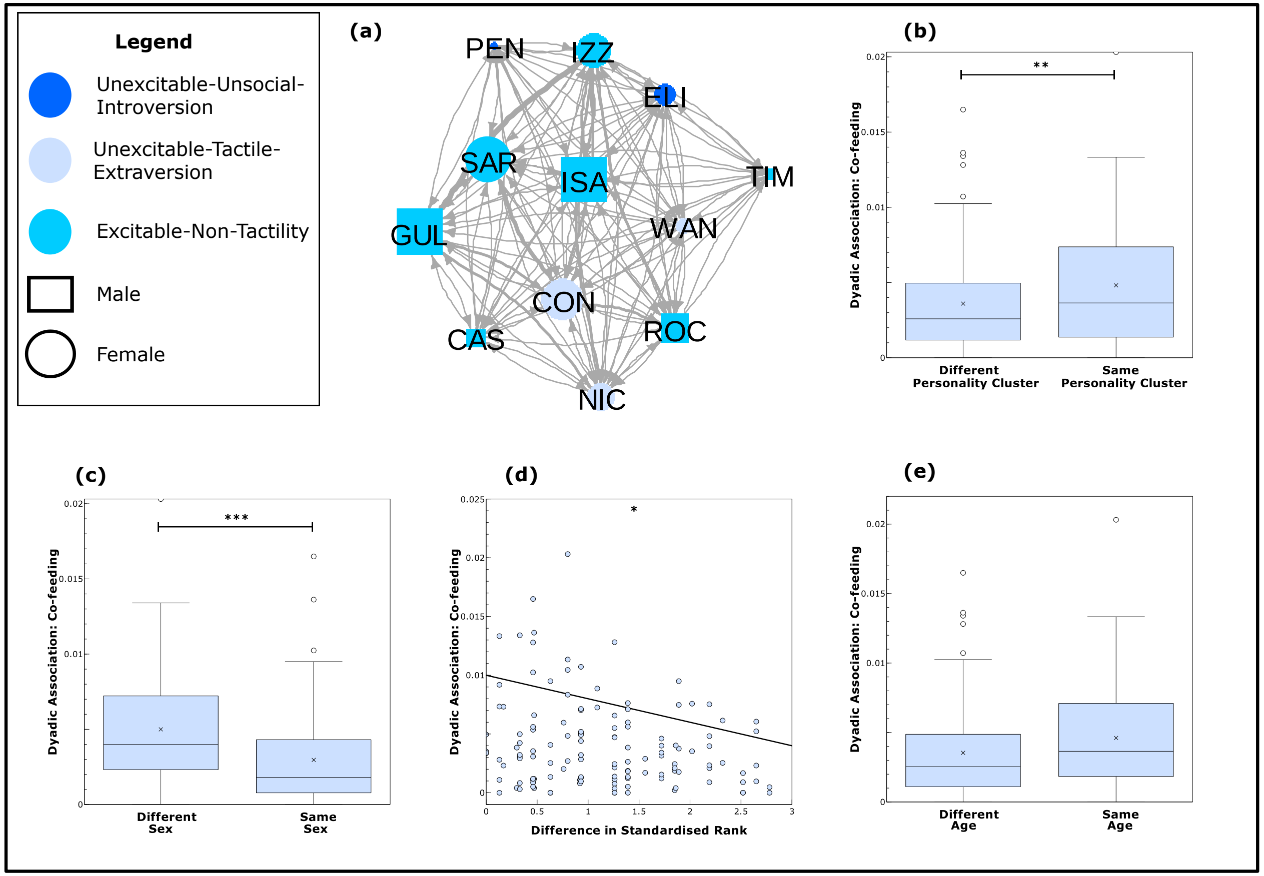


Figure 5.10: Patterns of homo- and heterophily in the Blue group co-feeding network. In the network graph (a), nodes are coloured according to personality cluster, shaped according sex (see legend inset) and sized according to rank (increasing size corresponding with higher rank) (n = 12). The inset graphs (b), (c), (d) and (e) illustrate relationships between dyadic co-feeding associations (proportion of time dyads co-fed relative to overall observation time) and differences in personality cluster, sex, rank and age respectively (n=132).

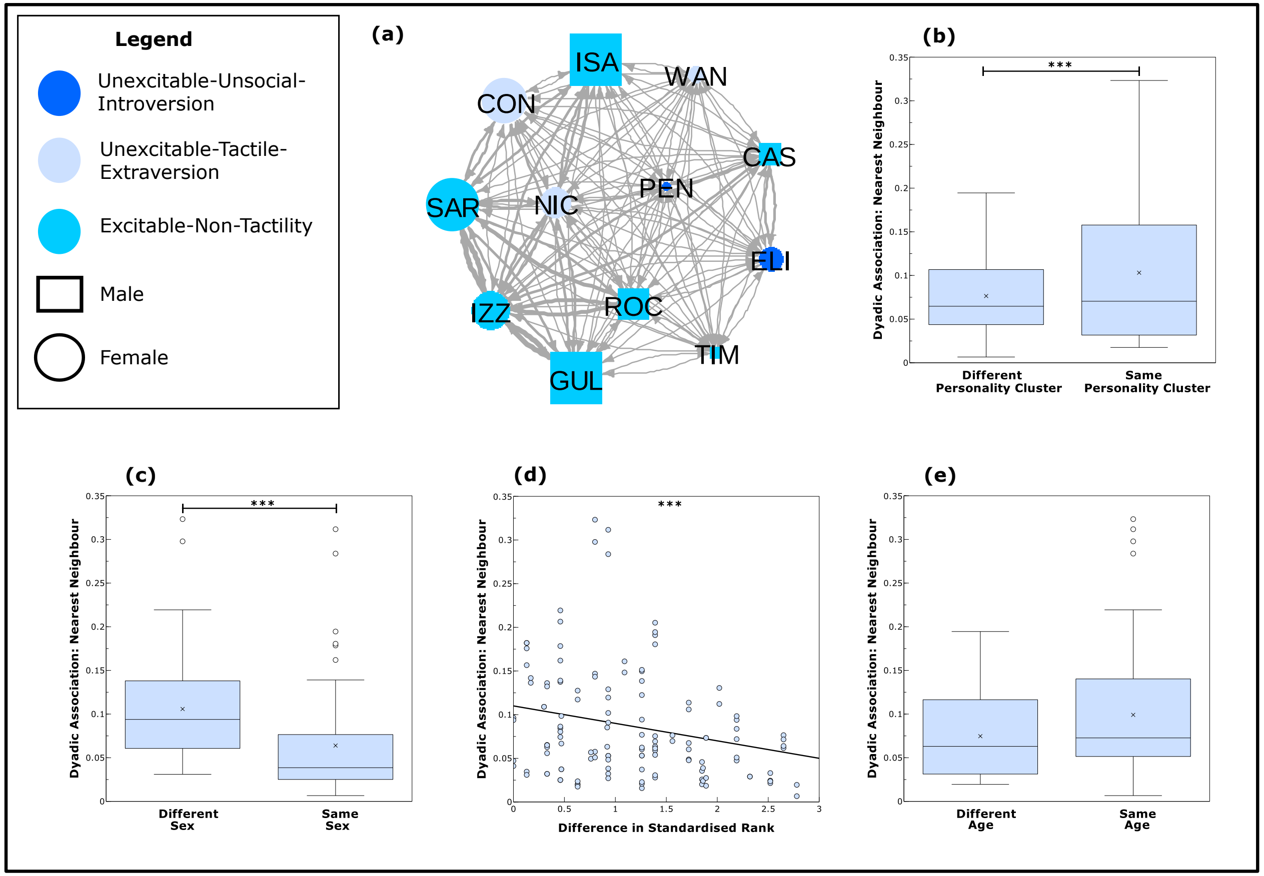


Figure 5.11: Patterns of homo- and heterophily in the Blue group nearest neighbour network. In the network graph (a), nodes are coloured according to personality cluster, shaped according sex (see legend inset) and sized according to rank (increasing size corresponding with higher rank) (n = 12). The inset graphs (b), (c), (d) and (e) illustrate relationships between dyadic neighbour associations (proportion of time dyads were neighbours relative to overall observation time) and differences in personality cluster, sex, rank and age respectively (n=132).

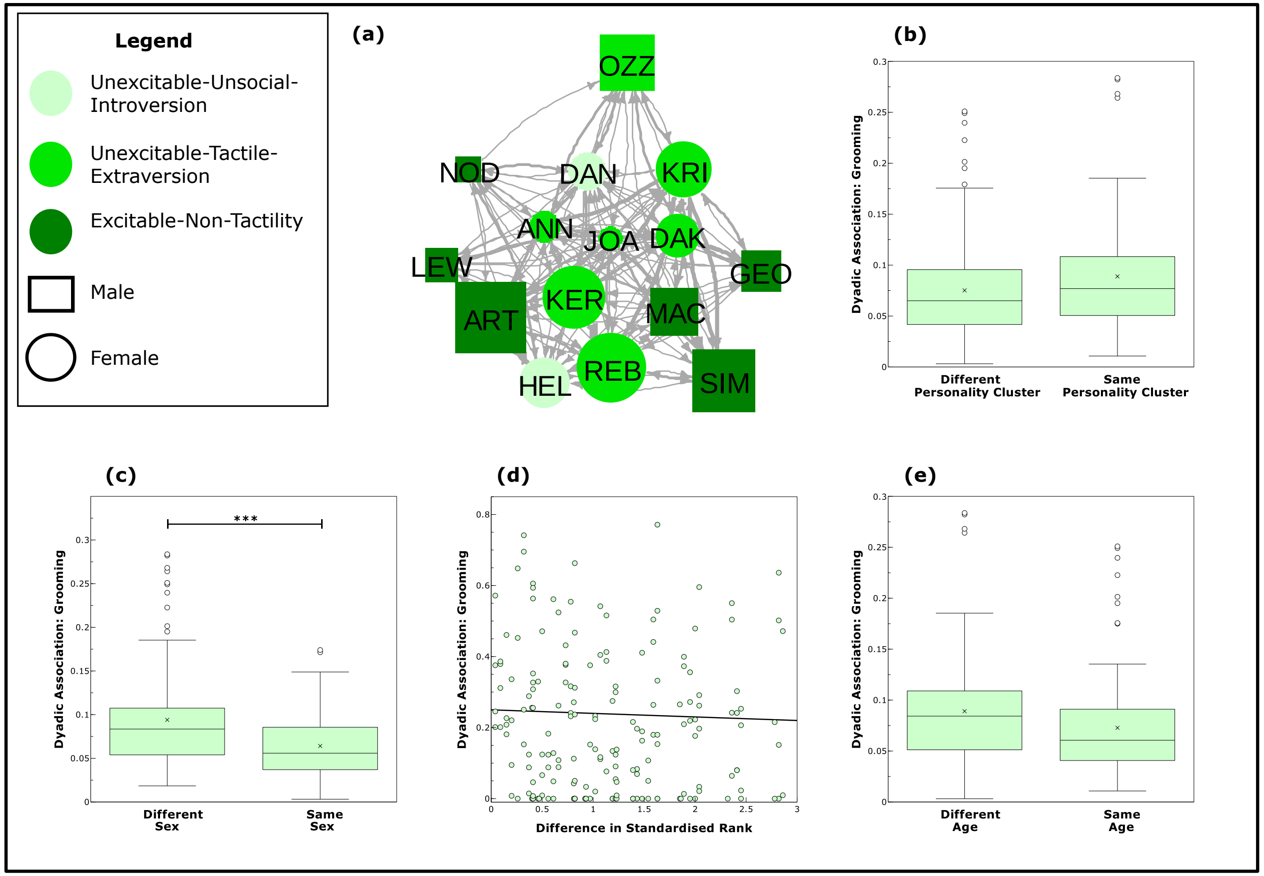


Figure 5.12: Patterns of homo- and heterophily in the Green group grooming network. In the network graph (a), nodes are coloured according to personality cluster, shaped according sex (see legend inset) and sized according to rank (increasing size corresponding with higher rank) (n = 12). The inset graphs (b), (c), (d) and (e) illustrate relationships between dyadic grooming associations (proportion of time dyads groomed relative to overall observation time) and differences in personality cluster, sex, rank and age respectively (n=210).

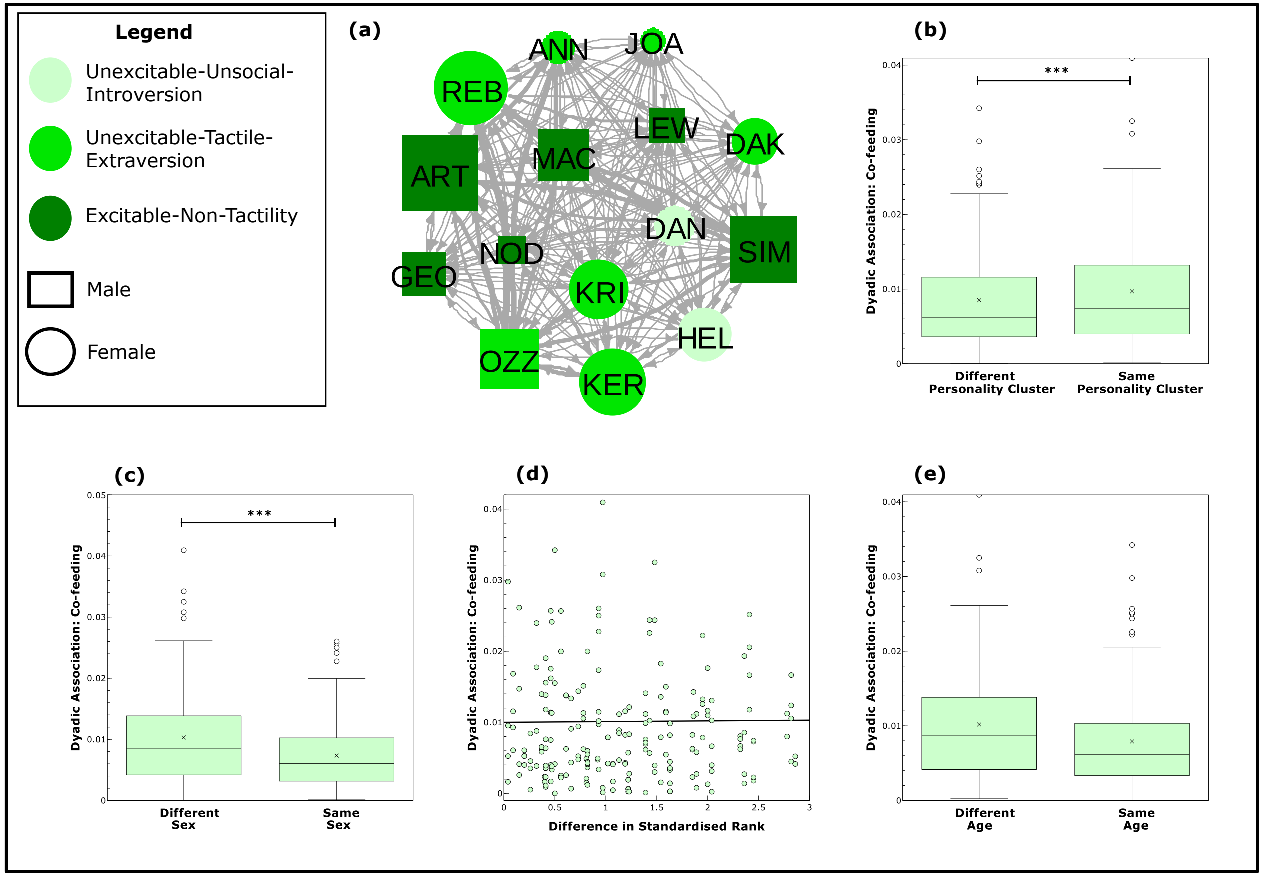


Figure 5.13: Patterns of homo- and heterophily in the Green group co-feeding network. In the network graph (a), nodes are coloured according to personality cluster, shaped according sex (see legend inset) and sized according to rank (increasing size corresponding with higher rank) (n = 12). The inset graphs (b), (c), (d) and (e) illustrate relationships between dyadic co-feeding associations (proportion of time dyads co-fed relative to overall observation time) and differences in personality cluster, sex, rank and age respectively (n=210).

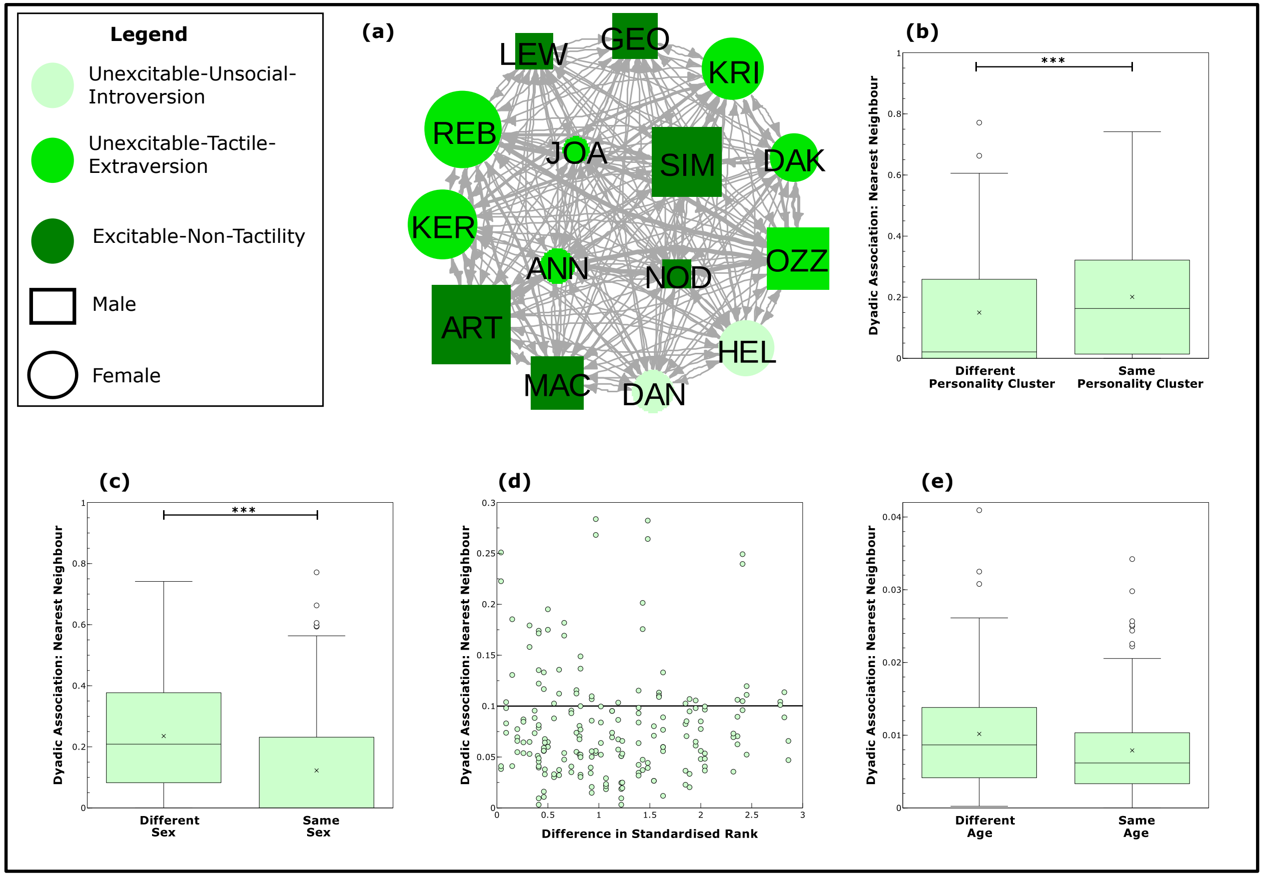


Figure 5.14: Patterns of homo- and heterophily in the Green group nearest neighbour network. In the network graph (a), nodes are coloured according to personality cluster, shaped according sex (see legend inset) and sized according to rank (increasing size corresponding with higher rank) (n = 12). The inset graphs (b), (c), (d) and (e) illustrate relationships between dyadic neighbour associations (proportion of time dyads were neighbours relative to overall observation time) and differences in personality cluster, sex, rank and age respectively (n=210).

As Exctiability was a key determinant construct for which personality cluster an individual occupied, evidence for personality homophily based on Exctiability scores was examined. Here, difference in Excitability was determined based on absolute differences in scores for this construct between individuals in dyads. For both groups, results indicated that individuals assort themselves within nearest neighbour networks according to Excitability score homophily (table 5.15; figure 5.15). No relationship between Excitability differences and the distribution of associations within grooming and co-feeding networks was found (tables 5.16 and 5.17).

Table 5.15: MRQAP results analysing the associations between dyads in the nearest neighbour networks of the (a) Blue group and (b) Green group. "Difference in …" refers to whether dyads had similar *Excitability* scores (continuous response calculated by differences in score for this personality), *sex* or *age* category (binary), or *rank* (continuous response calculated as difference in standardised rank). Coefficients from the regression analyses are reported, as well as the permutation results. Significant relationships are in bold.

(a) Blue Group

Variable	*B*	Proportion observed ß > randomised ß	Proportion observed ß < randomised ß	P-value
Intercept	0.09	1.00	0.00	0.00
Difference in Excitability	**<-0.00**	**0.02**	**0.98**	**0.04**
Difference in Sex	**-0.05**	**0.00**	**1.00**	**0.00**
Difference in Rank	**0.06**	**1.00**	**0.00**	**0.00**
Difference in Age	**0.02**	**0.98**	**0.03**	**0.04**

(b) Green Group

Variable	*B*	Proportion observed ß > randomised ß	Proportion observed ß < randomised ß	P-value
Intercept	0.12	1.00	0.00	0.00
Difference in Excitability	**-0.01**	**0.02**	**0.98**	**0.03**
Difference in Sex	**-0.05**	**0.00**	**1.00**	**0.00**
Difference in Rank	**0.01**	**0.98**	**0.02**	**0.04**
Difference in Age	-0.01	0.09	0.91	0.17

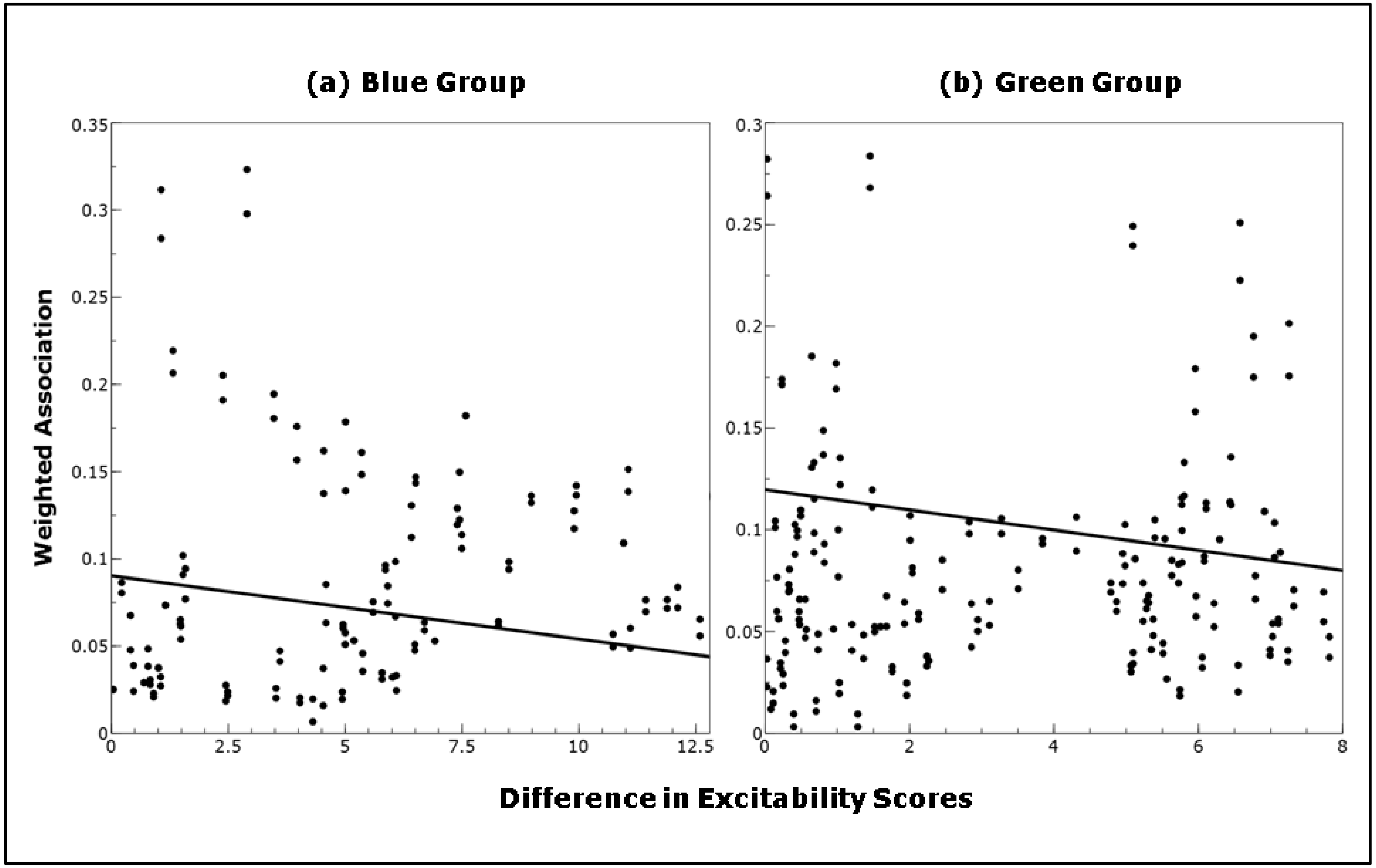


Figure 5.15: The relationship between weighted association between dyads and difference in Excitability scores between dyads within nearest neighbour networks for the (a) Blue group (n = 132) and (b) Green group (n = 210). The regression lines are calculated from the coefficients of the MRQAP results (table 5.14).

Table 5.16: MRQAP results analysing the associations between dyads in the grooming networks of the (a) Blue group and (b) Green group. “Difference in …” refers to whether dyads had similar *Excitability* scores (continuous response calculated by differences in score for this personality), *sex* or *age* category (binary), or *rank* (continuous response calculated as difference in standardised rank). Coefficients from the regression analyses are reported, as well as the permutation results. Significant relationships are in bold.

(a) Blue Group

Variable	*B*	Proportion observed ß > randomised ß	Proportion observed ß < randomised ß	P-value
Intercept	0.21	1.00	0.00	0.00
Difference in Excitability	<0.01	0.59	0.41	0.82
Difference in Sex	**-0.10**	**0.02**	**0.98**	**0.04**
Difference in Rank	0.06	0.95	0.05	0.10
Difference in Age	0.05	0.91	0.09	0.20

(b) Green Group

Variable	*B*	Proportion observed ß > randomised ß	Proportion observed ß < randomised ß	P-value
Intercept	0.25	1.00	0.00	0.00
Difference in Excitability	<-0.01	0.39	0.61	0.79
Difference in Sex	**-0.12**	**<0.01**	**>0.99**	**0.01**
Difference in Rank	0.01	0.67	0.33	0.69
Difference in Age	-0.02	0.26	0.74	0.48

Table 5.17: MRQAP results analysing the associations between dyads in the co-feeding networks of the (a) Blue group and (b) Green group. "Difference in …" refers to whether dyads had similar *Excitability* scores (continuous response calculated by differences in score for this personality), *sex* or *age* category (binary), or *rank* (continuous response calculated as difference in standardised rank). Coefficients from the regression analyses are reported, as well as the permutation results. Significant relationships are in bold.

(a) Blue Group

Variable	*B*	Proportion observed ß > randomised ß	Proportion observed ß < randomised ß	P-value
Intercept	<0.01	1.00	0.00	0.00
Difference in Excitability	<-0.01	0.20	0.80	0.39
Difference in Sex	**<-0.01**	**<0.01**	**>0.99**	**0.01**
Difference in Rank	**<0.01**	**1.00**	**0.00**	**0.00**
Difference in Age	<0.01	0.92	0.08	0.15

(b) Green Group

Variable	*B*	Proportion observed ß > randomised ß	Proportion observed ß < randomised ß	P-value
Intercept	1.00	1.00	0.00	0.00
Difference in Excitability	<-0.01	0.06	0.94	0.13
Difference in Sex	**<-0.01**	**0.01**	**0.99**	**0.02**
Difference in Rank	**<0.01**	**>0.99**	**<0.01**	**<0.01**
Difference in Age	<-0.01	0.09	0.91	0.17

5.2.5 Summary

Subjects were consistent in their social network positions across the whole study period within grooming, co-feeding and nearest neighbour networks, but not in aggression networks. Personality construct scores generally did not predict centrality or social network position, with two exceptions: individuals with higher Exploration scores tended to have higher individual clustering coefficients; and for males, higher Excitability scores were associated with lower eigenvector centrality, for females, the inverse relationship was observed. Personality homophily was observed in co-feeding and nearest neighbour networks, but not grooming networks. In nearest neighbour networks of both groups, individuals tended to associate with other individuals with similar Excitability scores. This same pattern was not observed in the grooming and co-feeding networks.

5.4 Discussion

This study addressed three research questions finding that (a) Barbary macaques are generally consistent in their social network positions, (b) Barbary macaque personality phenotype is not a strong predictor of social network position and (c) Barbary macaques socially associate according to personality homophily in co-feeding and nearest neighbour networks, but not grooming networks.

5.4.1 Personality and Social Network Positions

Determining the consistency of individual social network position is an important component of understanding the interplay between sociality and personality, yet has rarely been explored empirically (Aplin et al, 2015). In this study, wild Barbary macaques demonstrated consistency over time and context in social network position in three of the four networks analysed: grooming, co-feeding and nearest neighbour. Consistency in social network position has been observed in non-primate species, such as great tits (Aplin et al, 2015) and small spotted catsharks (*Scyliorhinus canicula*; Jacoby et al, 2014). In primates, studies to date have focused more on the consistency of social network structures or topologies rather than the positions of individuals within those networks (Barret et al, 2012; Brent et al, 2013c). Primate social systems are generally complex and their complexity has been proposed as a selective pressure on higher cognitive functions (Dunbar, 1998). How primates cope in these complex social environments is an ongoing focus for behavioural ecologists; the consistency found in this study, both in behaviour and social relationships, may be adaptive and aid social cohesion and stability (Flack et al, 2006). Barbary macaques are known to form long-term intra- and inter-sex dyadic social relationships (Young et al, 2014a; 2014b). Here, this study demonstrates that they also occupy long-term, stable network positions during periods of dynamic changes in ecological and social contexts, particularly the shifts between reproductive seasons and changes in dominance hierarchies (chapter 4). Whether personality is a consequence of sociality and social network position, as proposed by the social niche hypothesis (Bergmüller & Taborsky, 2010) or whether other proximate associations to personality, such as stress physiology and other evolutionary "states" (chapter 4; Wolf & Weissing, 2010) lead to behavioural patterns which shape sociality, cannot be inferred from the analysis presented here. However, this study shows a direct association between consistent personality phenotypes and consistent social network phenotypes, which may reflect functional outcomes of personality, which in turn may affect fitness (Dingemanse & Réale, 2005).

Consistency in network position was found in affiliative networks; the only network where subjects were not consistent in network position was the aggression network (even when the Green and Blue group were analysed separately to control for the less stable dominance hierarchy observed in the Green group during the study period). All networks were calculated across breeding seasons and in the context of several changes in dominance hierarchy structure, which combined are expected to significantly affect aggression rates and patterns: aggression is higher during breeding seasons due to competition for mating partners (Fooden, 2007; Young et al, 2014a), while dominance hierarchy instability leads to increased aggression as individuals vie for available rank positions (Rowel, 1974; Sapolsky, 2005). In terms of personality, a constituent behaviour of Barbary macaque Excitability is the amount of aggression directed to conspecifics (chapter 4). This implies that certain "excitable" subjects are being consistently aggressive, yet the lack of consistency in the aggression social network position implies that the direction of this aggression may fluctuate over time and context, unlike affiliative interactions where grooming, neighbour and co-feeding partners are more stable.

The interplay between social consistency in affiliation and social inconsistency in aggression may be important in maintaining overall group cohesion, with potential fitness consequences. Centrality within an aggression network has previously been linked to survival in Barbary macaques during an extremely cold winter, whereby aggressive interactions were suggested to stabilise affiliative relationships (Lehmann et al 2015). Aggression networks may be susceptible to greater influence of environmental changes (whether ecological or social), but the networks may also provide a framework for stability in other networks by compensating for these environmental changes (Barrett et al, 2012). Previous work in chacma baboons, a despotic species with high rates of aggression, supports this hypothesis (Barrett et al, 2012). The present study, as well as previous work in Barbary macaques (Lehmann et al, 2015), suggests the stabilising effect of aggression networks on affiliation networks may be an important mechanism in primate sociality regardless of social structure (i.e. despotic, as in chacma baboons or tolerant, as in Barbary macaques) and is an important avenue for future research in primate sociality.

Personality was not a strong predictor of social network position in wild Barbary macaques, with only two (out of seven) personality constructs found to be related to centrality in networks. Exploration was positively associated with individual clustering coefficients in grooming networks, while for male Barbary macaques, Excitability was negatively correlated with eigenvector centrality in nearest neighbour networks (for females, the relationship between Excitability and centrality appeared to be due to two highly "excitable" females). This suggests that "explorative" Barbary macaques are more "cliquish" in grooming networks, while "excitable" males are less central in nearest neighbour networks. Both Excitability and Exploration scores were positively correlated with physiological stress measures in males and females respectively. Occupying a less-connected but stable social position may be an adaptive strategy for certain individuals. Increased cliquishness (for females) or reduced centrality (for males) could thus represent conservative strategies to cope with being easily stressed or stress reactive, which is manifested behaviourally as Exploration or Excitability.

In humans and non-human primates, segregation of individuals into cliques within networks can increase in-group levels of cooperation and overall cohesion (Flack et al, 2006; Fehl et al, 2011), while centrality is linked to important processes such as social learning and information transfer (Claidière et al, 2013), but increases exposure to pathogen transmission (MacIntosh et al, 2012; Dubosq et al, 2016). Future research on Barbary macaques could address how personality is associated with centrality and these factors. For example, are "excitable", "non-central" Barbary macaque males poor at social learning, but have lower pathogen burden compared to conspecifics? This would help further understand the benefit/costs of personality in a socially complex species.

Barbary macaque Sociability, Tactility and Introversion, personality constructs characterised by social behaviours and interactions (or the lack of them), were not found to relate to social network positions. This may seem counterintuitive, but network position is an emergent property of networks. Dyadic interactions are the basis for constructing a network but then SNA analyses the networks themselves rather than the dyads. Thus measuring social integration using SNA avoids an issue with circularity, and also provides a novel perspective on group-level social structure and an individual's position within these structures. Social network position has been proposed as a personality phenotype in and of itself (Wilson et al, 2012). The low levels of synchronicity between "classically" quantified personality constructs and social network position in this study may support this concept. For example, a highly "tactile" individual could equally concentrate grooming on one favoured partner or multiple different partners, or even themselves (Tactility was characterised by durations of allo- and self-grooming). Introversion was quantified using trait rating; an individual scoring highly for Introversion may appear to researchers to be less socially integrated, yet the high density and connectivity of the observed networks mean that all individuals, even "introverted" individuals, on a network level, were well connected to other individuals. Quantifying personality is focused on an individual’s actions, not necessarily which individuals it is doing these actions with or to; SNA allows us to quantify consistent social phenotypes based on the direction and strength of an individual’s behaviour within a network. In this sense, SNA provides more of an insight into “social strategies”. Identifying proximate associations to and fitness consequences of these social strategies may reveal more compelling relationships than have been found in this project when focusing on individual personality constructs.

5.4.2 Homophily in Social Networks

Evidence was found supporting the social-niche hypothesis in Barbary macaques. Subjects demonstrated personality homophily in co-feeding and nearest neighbour social networks, i.e. macaques of a certain personality tend to associate with other macaques of the same personality in these networks. To assess personality homophily, composite personality profiles combining the multiple established personality constructs were created, providing novel evidence of how individual traits can combine and affect the social outcomes for individuals. A key personality construct in each of the broader personality profiles or clusters was Excitability and analyses demonstrated that in the nearest neighbour network, homophily for this single construct was observed in both groups.

In Barbary macaques, it appears that individuals with similar levels of Excitability associate more regularly with each other and that this personality construct influences the development of social niches. Unlike in chimpanzees, where personality homophily appears to be driven by affiliative personality characteristics (Massen & Koski, 2014), Barbary macaques appear to base preferential social relationships around “excitable” behaviour, which is comparable to assortment based on the bold/shy axis which has been explored in non-primate vertebrates (Croft et al, 2009; Aplin et al, 2013). Personality homophily was not observed in grooming networks, nor was personality heterophily, i.e. personality appeared to have no effect on assortment in grooming social networks. Arguably, choosing a grooming partner is a more direct social relationship than standing next to or eating with another individual (although in humans and other primates, proximity is reported to reflect important social bonds [Hill & Dunbar, 2003; Mitani & Amsler, 2003; Silk et al, 2003]). Grooming is also proposed as a tool or resource for social capital (Barrett et al, 1999). Therefore, the pattern observed may reflect the fact that individuals are passively attracted to individuals with the same personality in nearest neighbour and co-feeding networks, but actively disregard these preferences in choosing grooming partners. Alternatively, grooming partnerships are closely monitored by other group members, and high-ranking individuals can coerce low-ranking individuals into grooming them, making it hard to determine where true preferences lie in grooming networks (Kaburu & Newton-Fisher, 2015; 2016).

Personality homophily, as observed in co-feeding and nearest neighbour networks, may be adaptive if it improves cooperation by reducing the cognitive costs of choosing partners (Dall et al, 2004; Massen & Koski, 2014). Elsewhere, it has been proposed that heterogeneous mixing of personality phenotypes within groups can generate optimal foraging groups of “leaders” and “followers” (Johnstone & Manica, 2011). Therefore, assortment based on personality may have important implications for group-level dynamics, including movement, information and/or disease transfer (Aplin et al, 2013). Personality homophily in nearest neighbour and co-feeding networks suggests that individuals assort themselves according to personality during activities such as foraging and travelling, compared to the sedentary activity of grooming, where personality homophily was not observed. An important next step in our understanding of personality and the effects of personality homophily would be empirically quantifying the effect of social structures on factors such as cooperation or group movement. For example, future work in Barbary macaques and other species should explore whether individuals within a particular personality cluster usually dictate group movement. Individuals that associate more readily with one another based on personality may also cooperate to achieve tasks together, and these cliques of homogenous personalities could be more efficient at such tasks than cliques of heterogenous personalities. Social ties predict cooperation in primates (Melis et al, 2006), including Barbary macaques (Young et al, 2014a), yet the link between personality and cooperation is yet to be established. Personality homophily could also influence sexual selection if individuals which socialise also mate together (Schuett et al, 2011).

MRQAP was used to analyse homophily in this study. This analysis is calculated using matrices, but in fact analyses correlations between dyads across matrices, rather than assessing the network properties of individuals within the networks generated by these matrices. An alternative approach is Newman's assortment coefficient, which uses network properties, namely degree (number of edge connections) to calculate whether phenotypic variation explains variation in network position for individuals (Newman, 2003). Until recently this method was limited to binary networks; recent developments in software allow examinination of homophily based on phenotype in weighted networks (Farine, 2014). This approach may provide an insight into network-based homophily rather than the dyad-based homophily presented in this study, once again highlighting network-based “social strategies” rather than dyadic relationships.

In summary, Barbary macaques demonstrated consistency in social network measures, Exploration and Excitability were associated with social integration and centrality in social networks, and homophily for personality was found in co-feeding and nearest neighbour networks. These findings provide empirical support for the social-niche hypothesis for the evolution and maintenance of personality. Future work should focus on establishing a more concrete link between personality, social phenotypes and fitness in this species.

6| Discussion

Animal personality is one of the most topical subjects within modern behavioural and evolutionary ecology. In the last decade, the subject has generated a plethora of papers proposing adaptive models for personality's prevalence in animals, as well as papers highlighting the theoretical implications of personality in a range of fields within zoology. Extensive effort has been exerted in developing theoretical models, but as recently as 2015, researchers have highlighted the need for more empirical testing of these models and hypotheses pertaining to animal personality (DiRienzo & Montiglio, 2015), despite similar pleas almost a decade ago (Réale et al, 2007). The general aim of this thesis was to build on earlier empirical work by studying the causes and consequences of personality in *wild* Barbary macaques, an animal species with a complex behavioural repertoire, a diverse range of social interactions and one which occupies a varied and challenging ecological environment.

6.1 Summary of Key Findings

- The use of multi-method approaches to quantifying personality revealed that Barbary macaques have a more complex personality structure than previously assumed in studies where singular approaches were used.
- This personality structure is made up of seven constructs: Excitability, Sociability, Tactility, Confidence, Introversion, Boldness and Exploration.
- Tactility, characterised by the frequency of allo- and self-grooming, is a new personality construct, with no analogues seen in other animal studies to date.
- From a methodological perspective, this project confirmed the practicality of quantifying personality in wild primates using a multi-method approach.

- Barbary macaques demonstrated intra-individual consistency and inter-individual variation in their physiological stress levels. Inter-individual variation in physiological stress reactivity was observed; intra-individual consistency was not observed for this measure of stress physiology.
- The expression of three personality constructs (Excitability, Tactility and Exploration) was related to stress physiology, and the relationships between personality and physiology were sex- and in some cases, age-specific. These findings support the "state-dependent" hypothesis of personality.
- Barbary macaques were consistent across time and contexts in their affiliative social network positions, but highly variable in their aggression social network positions.
- Personality was not a strong predictor of social network position (centrality, i.e. social integration) in Barbary macaques. However, personality homophily was found in nearest neighbour and co-feeding networks, providing empirical evidence supporting the "social-niche" hypothesis of personality.
- Excitability expression was a key factor in this social segregation based on personality, which is significant as this personality construct was also linked to physiological stress. The results of chapters 4 and 5 link a personality construct (Excitability), proximate mechanism (stress physiology) and functional outcome (social assortment). This is the first time this has been found in wild animals, and the results support both the state-dependent and social-niche models for personality evolution and maintenance, while also demonstrating that these models and hypothetical processes may not be mutually exclusive.

6.2 What do Multi-Method Approaches Reveal about Personality Structure?

Personality is explored in animals for two key reasons: firstly, to advance our understanding of the behavioural ecology of a particular species, and secondly, to explore adaptive models to understand why personality exists and its evolutionary history. Cross-species and cross-population comparative studies have been hampered by the inconsistent methods used between studies (Smith & Blumstein, 2008; Uher, 2008; Carter et al, 2012; Carter et al, 2013). Furthermore, most studies have focused on a limited number of personality constructs within a species, when evidence suggests animals may have multi-faceted personality structures, and each facet should be understood in terms of its proximate associations and functional outcomes (Dingemanse & Réale, 2005). Therefore, one of the aims and outputs of this project was to produce an empirical quantification of personality in Barbary macaques which was as comprehensive as possible, to demonstrate whether a multi-method approach was plausible and to examine if it would be beneficial for future personality research.

There are three main methods for quantifying personality in animals (experimental assays, behavioural coding and subjective trait assessment) and in this project, all three were used. Some personality constructs generated by behavioural coding correlated positively with those generated by subjective trait assessments (Excitability and Sociability were both identified by the two methodologies). However, both of these methods generated independent personality constructs which were uncorrelated with those derived from another method and would not have been found if a single approach had been used (Tactility in the case of behavioural coding; Confidence and Introversion in the case of subjective trait assessments). Similarly, the two experimental assays (playback and novel object experiments) generated personality constructs which were independent of each other, and independent of the constructs generated by the non-experimental methods. Behavioural coding takes a “bottom up” approach to measuring personality by looking at correlations in behaviour over time and context, while subjective trait assessments take a “top down” approach and have the potential to capture elements of personality that may be infrequently captured in behavioural observations. Experimental assays add the additional advantage of simulating infrequent events which may result in the expression of personality.

The findings of this project demonstrate that a multi-method approach generates more personality constructs than using singular approaches. But are more constructs necessarily better? Previous Barbary macaque research found only four personality constructs (Konečná et al, 2012; Adams et al, 2015). In this project, Barbary macaques were found to have more constructs than have been described in any other species to date. It is unlikely that Barbary macaques have more complex personality structures than any other animal; the more parsimonious explanation is that each quantification method is so distinct from another, one method will invariably capture an element of personality which is not possible with one of the other quantification methods. This is clear when looking at the assays of Boldness and Exploration used in this project. These are the most well studied personality constructs in animal research (Smith & Blumstein, 2008; Carere & Maestripieri, 2013) and require experimental assays to be quantified. In chacma baboons (*Papio ursinus*), boldness and exploration were distinct personality constructs which required different experimental approaches (simulated predation threat and novel objects respectively) in order to be quantified (Carter et al, 2012). The same was observed for Barbary macaques in this study. These findings support the "Reinforcement Sensitivity Theory" of personality, which postulates that personality is composed of components of reactivity (Corr et al, 1995). Within this framework, personality is expressed based on the nature of presented stimuli: aversive, novel/uncertain or positive (Gray & McNaughton, 2000). If making the argument that more constructs equates to a more "complete" quantification of personality, then the present project should also have included an experimental approach using a "positive" stimulus, but this would have been logistically impossible given time constraints.

Both behavioural coding and subjective trait assessments are rooted in the concept of personality being made up of several constructs expressed through behavioural traits, and therefore, we should expect some correlations between the constructs generated by the two methods. Experimental approaches have been developed based on a concept of personality being a reactive tendency. Mixing quantification methods rooted in different concepts of personality is perhaps always going to generate a diversity of personality constructs. Achieving a characterisation of personality structure that has "functional equivalence" (Uher, 2008; Carter et al, 2013) could be achieved in incremental steps rather than in a single study whereby each study uses methods based on one concept of personality per study (i.e. using both behavioural coding and trait rating together, or just using experimental assays). This then allows the researcher the opportunity to explore in greater detail how the generated personality constructs identified are related to the behavioural ecology of the species rather than focusing so much effort on personality quantification in and of itself.

In terms of relating personality to proximate associations and functional outcomes, neither of the trait rating-derived constructs (Confidence and Introversion) were related to stress physiology or sociality measures. The only relationships observed were with two behavioural coding-derived traits, Excitability and Tactility, and with experimentally-derived Exploration. The subjective trait assessments were not conducted concurrently with the observational (experimental and non-experimental) and physiological data collection. Arguably, Confidence and Introversion may be related to physiological and sociality measures not examined in this study. However, these results may also suggest that, statistically, having to reduce trait rating-derived construct scores, physiological and sociality measures to a single mean value per subject, may reduce the variation between subjects and thus make it difficult to identify how these factors relate to one another. As such, researchers should consider their aims when choosing the methods to adopt when conducting personality research: multi-method approaches may facilitate cross-species comparisons, but behavioural coding, and perhaps experimental assays, may be sufficient for exploring relationships between personality, physiology and sociality. As human personality quantification is almost exclusively conducted using self-reporting questionnaires (Thalmayer et al, 2011), the findings in this project and other multi-method animal personality quantification studies suggest that applying behavioural coding or experimental assays to humans may reveal more constructs of human personality than have been previously identified.

On a practical level, this project has shown that a multi-method approach to quantifying personality is possible when working in challenging field conditions and with unpredictable, wild animal subjects. With around 90% of primate species’ personality structures remaining to be quantified (Freeman & Gosling, 2010), it is important that, in future research, primatologists use methods which maximise potential for taxonomic comparison but also allow for accurate exploration of proximate associations and functional outcomes of personality. For maximising taxonomic comparisons, and based on current trends in the literature, researchers should be using subjective trait assessments and behavioural coding concurrently. For exploring the behavioural ecology and endocrinology of personality, behavioural coding and experimental approaches should be used in the quantification of personality.

6.3 The Prosocial Personality of Barbary Macaques

By expanding our understanding of the personality structure of Barbary macaques, this project also improves our knowledge of the social style of the species. With the exception of Exploration, all other personality constructs were characterised by social interactions between Barbary macaques. Of these "social" personality constructs, only Introversion and Confidence were solely defined by anti-social interactions. Even personality constructs characterised partly by aggression, i.e. Excitability and Boldness, also had short-term affiliation variables as constituent behaviours. In the "Big Five" model of human personality, "prosocial" personality (i.e. personality defined by positive social interactions with others) is divided between "Extraversion" and "Agreeableness" (McCrae & John, 1992). These two broad prosocial personality constructs, or analogues of them, also tend to exist in non-human great apes (Gold & Maple, 1994; King & Figuerdo, 1997; Weiss et al 2011), whereas in most macaque species, there tends to be a single prosocial personality construct (Adams et al, 2015). Why might Barbary macaques have a personality structure more strongly characterised by prosociality when compared to other macaque species? This may be a methodological issue, whereby the mutli-method approach used in this study has revealed more about the personality of Barbary macaques than has been achieved in other macaque studies (section 6.2). Alternatively, Barbary macaques have been characterised as "tolerant" or "egalitarian" when compared to many of their despotic congenics (Thierry et al, 2000; Wendland et al, 2006), and this is partially reflected in the Barbary macaque personality constructs found in this project. Barbary macaques experience winters with extreme cold and snow and summers of extreme heat and drought (Majolo et al, 2013), and in previous studies, individuals with strong social relationships have higher survival rates during climatic extremes compared to more socially isolated individuals (McFarland & Majolo, 2013). Therefore, there may be a selective pressure on prosociality. However, Japanese macaques (*Macaca fuscata*) also occupy a habitat with extremely cold winters, yet the social structure of this species is considered to be extremely despotic (Thierry et al, 2000) and the species appears to lack the diversity of prosocial personality that is present in Barbary macaques (Adams et al, 2015). Research on Japanese macaque personality has used only one method for quantifying personality constructs (trait rating; Adams et al, 2015). Incorporating behavioural coding and/or experimental assays may help reveal just how divergent Japanese and Barbary macaque personality structure is, and how this relates to social structure.

To date, Tactility is a personality construct unique to Barbary macaques. Garai et al (2016) identified the personality "Grooming" in wild bonobos (*Pan paniscus*), characterised by the frequency of allogrooming interactions and social interactions with conspecifics, whereas in Barbary macaques, Tactility was characterised solely by the frequency of allogrooming and self-grooming, i.e. independent of other social interactions. Tactility, or an analogue of it, has not been identified in previous Barbary macaque personality studies. These studies used subjective trait assessments and questionnaires and once again, it may be that single approaches to quantifying personality may be unsuited to capturing this important component of sociality and personality in a species (Konečná et al, 2012; Adams et al, 2015). Still, it is interesting that both bonobos and Barbary macaques, "tolerant" species compared to other species within each of their genera (Thierry et al, 2000; Wendland et al, 2006; Clay et al, 2016), are the only primates identified with a personality construct centred on the socially important interaction of grooming. Societal differences between chimpanzees and bonobos are proposed to derive from bonobos occupying a habitat with larger food patches and less competition from other primate species compared to the habitat of chimpanzees (Hare et al, 2012). Barbary macaques are the only extant primates in Northern Africa and in terms of diet, favour terrestrial foods such as grass, or widely distributed fruits, such as acorns (Majolo et al, 2013). This relative isolation and lack of clumped food resources may afford more time for prosocial interactions. Therefore, quantifying personality constructs in modern primates may provide a window on their evolutionary and ecological history and help us understand adaptive radiation within a genus.

6.4 Causes and Consequences of Personality

The second major aim of this project was to examine the relationship between stress physiology and personality in Barbary macaques in order to examine the state-dependent hypothesis. This posits that personality is generated and maintained by inter-individual variation in evolutionarily-strategic states (e.g. body size, health etc.), and that these states are stable enough to be associated with intra-individual consistency in behaviour (Biro & Stamps, 2008). In Barbary macaques, stress physiology varied between individuals and was stable enough to be a potential personality-associated state under the state-dependent hypothesis.

Physiological stress level (mean fGC concentration) was only weakly (small coefficient in the model) positively correlated with one personality construct, Exploration, in females. The observed relationships between the expressions of Excitability and Tactility and physiological stress *reactivity* were stronger (larger model coefficients), especially in males. Results suggest that behavioural phenotypes may be more closely, mechanistically linked to physiological stress *reactivity*, rather than overall stress *levels*, at least in Barbary macaque males (figure 6.1). Personality-associated behaviours may manifest in reaction to changes in physiological stress level, and these behaviours may serve to return physiological stress to baseline levels. For example, in Barbary macaque males, being highly stress reactive (i.e. more susceptible to stressors and thus variation in physiological stress) may require "excitable" behaviours in order to achieve some stability in physiological stress level. This is in keeping with well-established theories regarding personality as a "coping-style" for different levels of physiological stress reactivity as opposed to baseline levels of stress (Koolhaas et al, 1999). The absence of this type of relationship in females requires further exploration. Montiglio et al (2015), proposed that female wild chipmunks (*Tamias striatus*), downregulate physiological stress during pregnancy to maximise current reproduction by reducing energy used in stress responses. All Barbary macaque females, with the exception of the two elderly adult females, became pregnant during the course of the current study and further, were pregnant during much of the data collection of this project. Analysing the relationship between female Barbary macaque personality and physiological stress outside of the mating or birth seasons could confirm whether these females also downregulate physiological stress to meet reproductive demands and the impact this has on behavioural repertoires. This would also help improve our understanding of how flexible personality is over particular timeframes and at different life history stages.

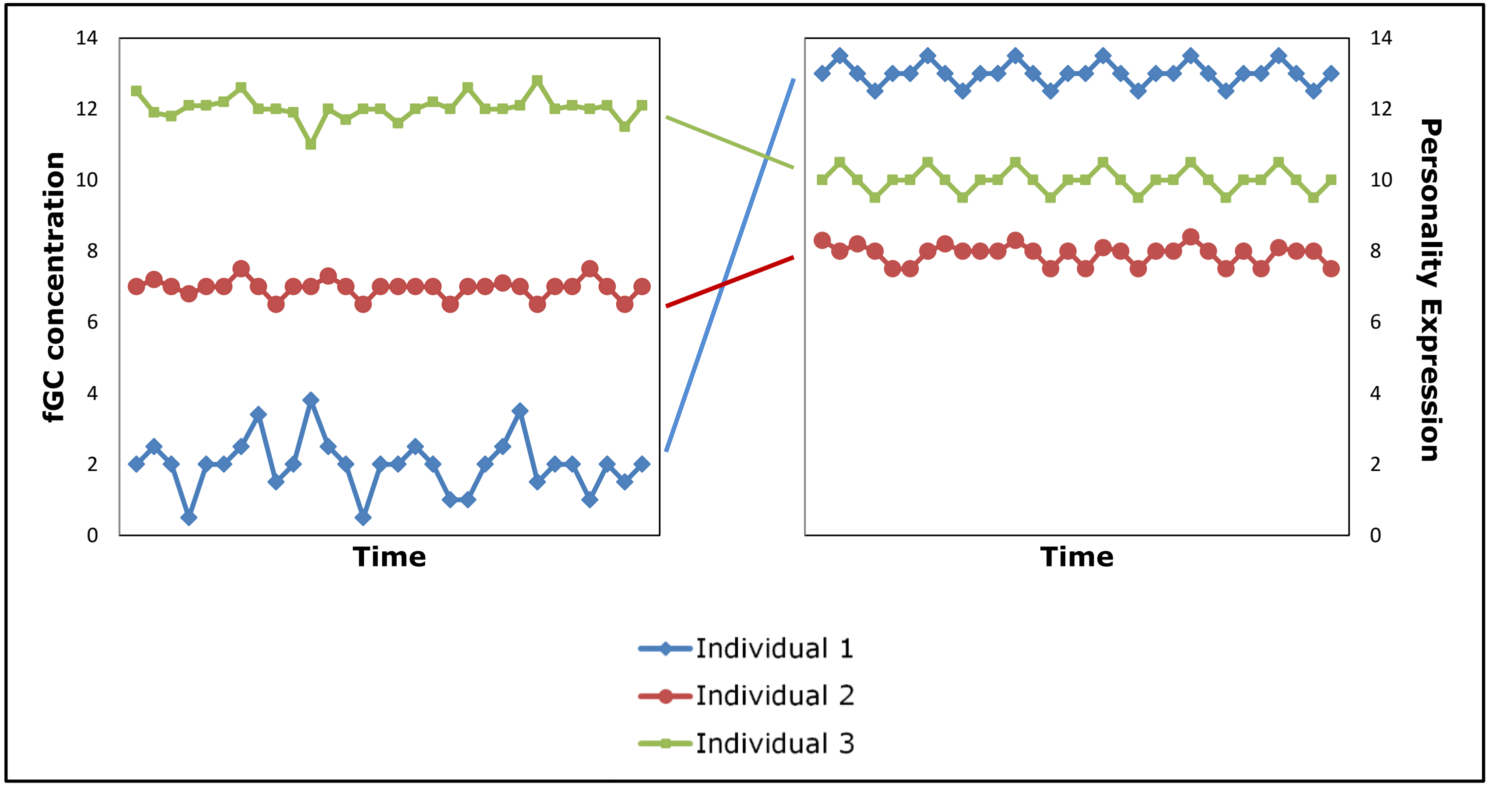


Figure 6.1: Diagrammatic representation of suggested link between personality and stress *reactivity* (variation in fGC concentration) rather than stress *level* (actual fGC concentrations). All three hypothetical individuals vary in their overall stress levels (fGC concentration) and stress reactivity (fGCcv; individual 2 has the lowest fGCcv, individual 1 the highest). Stress level has no clear relationship with personality expression; however, individual 1 is the most stress reactive, and for this theoretical personality construct, as with Excitability in male Barbary macaques, higher stress reactivity is associated with greater expression of personality.

In Barbary macaques, as well as being sex-specific, the relationship between stress physiology and personality expression can in some cases be affected by rank or age. This supports the "pace-of-life syndrome" hypothesis for personality, i.e. that individuals vary in behaviour because of variation in state, and these states are associated with life-history stage. Some states are more stable than others; for example, there are sex differences in evolutionary strategies and in mammals, sex is permanent (Wolf & Weissing, 2010). However, endocrine responses are markedly less stable and there is increasing evidence that not only do physiological stress responses vary with age, they also vary according to life experience (Slavich & Cole, 2013; Dettmer et al 2016). In this study, the expression of the Tactility construct in males was related to an interaction between stress physiology and age. For all males, higher physiological stress reactivity was associated with lower Tactility scores; elderly, stress-reactive males had lower Tactility scores than adult, stress-reactive subjects. Behavioural inflexibility may appear maladaptive (the example of fishing spiders, section 1.2; Johnson & Sih, 2005), but state-dependent behaviour may be adaptive if organisms demonstrate the "best behaviour" for their given state and experience (Sih et al, 2015). For elderly males, responses to variation in stress reactivity may differ from their younger conspecifics due physical limitations, motivations or fitness outcomes related to their life-history stage. The next step for confirming this adaptive model would be a longitudinal study of Barbary macaques, or another species with distinctive and, in order to measure behavioural consistency within that period, extended life history stages. Tracking personality throughout life history in conjunction with quantifying direct fitness outcomes (such as mating or reproductive success) would reveal more about personality as an adaptation than the snapshot of the relationship between personality, life-history and stress physiology provided by this study.

In chapter 5 of this thesis, functional outcomes of personality expression were explored by examining how personality is associated with sociality. Barbary macaques tended to socialise with conspecifics with similar personalities, supporting the "social niche" hypothesis, which proposes that personality evolves and is maintained when individuals occupy particular social roles within a group (Bergmüller & Taborsky, 2010). In group-living primates with a dominance hierarchy, we might expect such social segregation to occur based on rank (Janson, 1990; Murray et al, 2007; Naud et al, 2016). However, across the two study groups, rank was an inconsistent predictor of social assortment, whereas for both groups, personality homophily was found in nearest neighbour and co-feeding networks.

Excitability appeared to shape social niches in both study groups, with individuals of a similar level of Excitability tending to socialise more than individuals with different levels of Excitability. This may be significant as, in male Barbary macaques at least, Excitability is also related to physiological stress. If more "excitable" individuals associate more readily with one another, or are forced to associate as less "excitable" individuals avoid them, individuals within the highly "excitable" social circle may experience erraticism in physiological stress as a consequence of socialising with behaviourally and physiologically erratic individuals. In many non-primate species, it has been shown that shyer and less active individuals tend to avoid bolder or highly active individuals (Croft et al, 2009; Aplin et al, 2013). A similar pattern is apparent in Barbary macaques and is apparently linked to stress physiology. In this respect, the results presented here may be the first to link personality, stress physiology and social-niche segregation in a wild animal species.

How and why animals form and maintain social groups remains a focus for behavioural and evolutionary ecologists and personality presents a new paradigm through which to explore and understand social interactions and relationships (Rubenstein & Kealey, 2012; Clutton-Brock, 2016). Results from this thesis suggest personality arises from, or perhaps causes, social segregation, and that the construct of personality most involved in these processes (Excitability) is linked to stress physiology. This study also shows that this personality/physiology social segregation leads to a degree of social stability, as indicated by the consistent social network positions of individuals. The stability of social connections may be important in mitigating long-term physiological stress (Sapolsky, 2005; Young et al, 2014a), and this reduction in stress may then lead to positive fitness outcomes such as increased survival or higher reproductive output (Silk et al, 2009). Therefore, personality may be adaptive if it helps maintain social stability for individuals through the formation of social niches.

As indicated previously, stress physiology and its relationship to personality expression appear to vary with life-history stage. Ideally, future work would investigate links between personality, physiology and sociality throughout development to help us understand how personality is related to social stability and how social stability relates to physiological processes in the same way that primate research has helped us understand how rank affects social relationships and health over the course of a lifetime (Sapolsky et al, 2005; Silk et al, 2009; Silk et al, 2010). King et al (2015) demonstrated that personality may be malleable to social conformity in a series of experiments with captive Gouldian finches (*Erythrura gouldiae*): individuals that spent time with especially “bold” conspecifics would themselves become bolder. Performing similar experiments is neither practical nor ethical in wild primates. However, sudden changes to social structure do occur in wild primates, either through death, dispersal or fission-fusion social mechanisms (Symington, 1990; Amici et al, 2008; Alberts, 2012). It would be interesting to use the methods described in this study of Barbary macaques to test whether personality homophily is present in other animals where social structures are more fluid, and how this affects measures of intra-individual consistency in behaviour, as well as stress physiology. Other populations of Barbary macaques have been observed to have fission-fusion social structures (Ménard & Vallet, 1993), therefore, within-species, inter-population comparisons may also provide important information about how variation in social structure and stability may be related to personality. For example, following fission, are parties with a more homogenous mix of personality more stable (either in terms of duration of the party or the level of aggression within that party) than those with a more heterogenous mix of personality? Does the presence of an “excitable” individual among less “excitable” individuals affect stress physiology for either the “excitable” individual or those around it? When dispersing, do individuals initially disperse into sub-groups of individuals with similar personalities to themselves? Personality homophily appears to be common in vertebrates, including humans (Klohnen et al, 2005; Pike et al, 2008; Selfhout et al, 2010; Aplin et al, 2013; Massen & Koski, 2014). This is one of the first studies to concurrently link personality homophily to a physiological process (hormonal stress response) and thus directly link the state-dependent and social-niche adaptive models for the evolution and maintenance of personality.

6.5 Future Behavioural and Endocrinological Studies of Personality in Wild Animals

Barbary macaque personality was related to both baseline levels of physiological stress and to physiological stress reactivity. The latter was calculated using a new measure, fGCcv, or "demonstrated reactive scope" (MacLarnon et al, 2015). Previous work linking personality to stress physiology has largely focused on associating overall means in hormonal stress levels to personality (Carere & Maestripieri, 2013). Former research measuring stress reactivity has adopted invasive methodologies, such as serum sampling immediately after a stressful event. This stressful event may even be manufactured by the investigator rather than reflecting a natural occurrence, and hence may not reflect the range of stress reactivity in a natural setting (Wingfield et al, 1994; Koolhaas et al, 1999; Sapolsky 2005). "Demonstrated reactive scope" is a non-invasive measure of reactivity and generates a metric of reactivity which is cross-species comparable, i.e. a percentage representing variation in physiological stress rather than a concentration of glucocorticoid metabolites which may vary in magnitude between studies depending on the size of the species or methods used to determine the concentration (MacLarnon et al, 2015).

Time lags associated with the metabolism and transfer of hormones into excreta previously limited researchers from associating specific behaviours or events with hormonal outputs. However, detailed understanding of these time lags (based on validation studies performed in captive studies) and the ability to collect and store repeated samples from individuals have significantly improved the accuracy with which researchers can measure hormone reactivity (Crockford et al, 2013; Wittig et al, 2015). Where such sampling regimes are practical, they should be encouraged and could significantly improve our understanding of personality. For example, Wittig et al (2015) demonstrated that in chimpanzees (*Pan troglodytes*), repeated measure sampling could identify peaks in stress (identified using urinary cortisol) associated with aggressive interactions with conspecifics. For personality research, inter-individual differences in the relative magnitude of stress peaks following a stressor could be identified, and tested against inter-individual differences in personality. Intra-individual consistency in the relative magnitude of these stress peaks could then be explored. Repeated measure sampling could also investigate the speed of stress reactivity (i.e. how quickly individuals return to a baseline level following a stress peak); inter-individual variation in the speed of endocrine reactivity has been proposed as a mechanistic link to inter-individual variation in personality expression, but is yet to be studied empirically in wild animals using non-invasive meothds (Taff & Visoutek, 2016). Furthermore, if experimental assays are used to quantify personality, hormonal correlates to behavioural responses to stimuli could be thoroughly explored by sampling subjects after an experiment to detect changes in hormone activity. In this study, female Exploration scores were higher in individuals with higher overall levels of physiological stress. In other animal studies, boldness has been linked to stress physiology (Montiglio et al, 2012; 2015; Fürtbauer et al, 2015). Barbary macaque stress responses to a threatening stimulus may involve rapid and specific hormonal reactions which were not detectable using the sampling regime of this study.

Within animal personality research, it remains a challenge to disentangle cause and effect when examining relationships between personality and hormones and social outcomes. All three are theoretically involved in feedback loops with one and other, so that it is challenging to address whether personality is a consequence of endocrinology and sociality, or whether being of a particular personality places an individual in social situations or environments which result in particular endocrine responses. The best way to address this for future research would be to trace these associations throughout development or across varying social or ecological environments. For endocrinology, there have been a number of recent publications demonstrating that early-life experience and developmental factors are related to hormonal functioning and physiology later in life (Winslow et al, 2003; Branchi et al, 2013; Dettmer et al, 2016). Furthermore, social or environmental factors appear to influence how genes are expressed, which in turn affects the expression of hormones (Cole, 2009). Modern genotyping technologies also make it possible to study the genetic template an individual inherits in relation to endocrinology and how this is reflected in hormone expression (Slavich & Cole, 2013; Dobson & Brent, 2013). Allelic variations and single nucleotide polymorphisms (SNPs) are a current focus within genetics and endocrinology, whereby it is proposed that variation in alleles transcribing hormones generates variation between individuals in their ability to produce hormones with a subsequent effect on behaviour (Dobson & Brent, 2013). Meta-analyses examining whether SNPs lead to variation in behaviour have had mixed results (Ficks & Waldman, 2013; Vassos et al, 2014), and this is proposed to be an effect of “gene x environment” interactions (Kalbitzer et al, 2016). By genotyping individuals, and then tracking whether and how the relationship between personality and endocrine responses varies over different social gradients, ecological environments and life-history stages, researchers may be able to more accurately assess whether personality is the cause or consequence of social environment and/or physiology.

Hormones do not act in isolation, but pluralistically and in complex feedback loops with other hormones (Crespi, 2015). In Barbary macaques, three out of seven personality constructs were associated with the physiological stress response in one sex or both. It is possible that the other four personality constructs may be related to other endocrine processes, or the relationship of their physiological stress response to other hormonal processes. A number of candidate personality-associated hormones can be quantified from primate excreta. The peptide hormone oxytocin, which can be assayed from urine, is implicated in social bonding: in a number of vertebrate species, social bonding behaviours such as affiliative touching, grooming and shared gazes are associated with elevated endogenous production of oxytocin (Ross & Young, 2009; Crockford et al, 2013). Testosterone, which can be assayed from either faeces or urine, is involved in mediating responses to dominance interactions or social challenges (Wingfield et al, 1990). The "dual-hormone" hypothesis states that the ratio of cortisol and testosterone should predict affiliative interactions through feedback loops reducing overall aggression and stress levels (Zilioli et al, 2014). Oxytocin also appears to be dynamically related to cortisol and testosterone and is involved in a number of proposed feedback loops related to social anxiety and motivation for social interaction (Crespi, 2015). It is now also possible to monitor thyroid hormones in wild animals and primates via faecal samples, providing a non-invasive method to monitor metabolic activity (Wasser et al, 2010; Cristóbal-Azkarate et al, 2016). Metabolism has been proposed as a personality-associated state (Careau et al, 2008; Careau & Garland, 2012), yet, to date few studies have been able to empirically test this, and those that have required invasive methodologies (Careau et al, 2015). Overall, relating personality to endocrinology is very much in its infancy, and examining other hormones, and multiple hormones concurrently, are promising further avenues of research in order to fully understand the causes and consequences of personality.

6.6 Conclusions and Outlook

Barbary macaques are an endangered species (IUCN, 2012), and the research presented in this study may have some conservation implications. Barbary macaques face three linked, existential threats: the pet trade, habitat loss and human-macaque interactions (van Lavieren & Wich, 2010). The reductions in habitat, naturally occurring food resources and human encroachment through tourist or pastoral activity are bringing Barbary macaques into more frequent contact with human populations (Ménard et al, 2014). This proximity to humans increases the risk of poaching of infants for the pet trade (van Lavieren & Wich, 2010). It also increases the risk of zoonosis between the macaques and humans, and recent evidence shows groups of Barbary macaques that interact more frequently with humans have a greater diversity of endogenous parasites (Borg et al, 2014). Furthermore, Barbary macaques which interact with humans have poorer health outcomes, including obesity and elevated physiological stress levels (Maréchal et al, 2011; 2016).

This study shows that Barbary macaques have varied personalities and these may reflect behavioural strategies for coping with the social and ecological environment. Based on the diversity of Barbary macaque personality demonstrated in this study, it is anticipated that personality may predict which individuals interact most frequently with humans. In addition, if individual personalities shape group-level dynamics such as group movement, personality composition within a group may be able to predict which groups are more likely to move into more human-disturbed areas. Further research about the effect of personality on responses to human activity might inform conservation strategies, such as vaccination programmes or monitoring of groups or macaque mothers within groups that may be most vulnerable to poaching of infants. Reintroductions of poached Barbary macaques have been attempted within Morocco; Waters et al, (2016) reintroduced a poached infant into the Green group studied in this project. The authors claim the infant was "adopted" by one adult male, NOD. The infant survived in the group for over a year before dying during winter. Personality may predict individuals which are more likely to "adopt" reintroduced individuals. For example, NOD was an elderly male, with higher Exploration scores than most other males. Finally, demonstrating to local people that each Barbary macaque has a unique identity and personality may help improve attitudes to the animals and create a more complete understanding of how complex this species is and its value to local ecology.

The aims of this thesis were somewhat hampered by permit issues. Nevertheless, the results revealed the complexity of personality in wild Barbary macaques and provided empirical evidence supporting adaptive models for the evolution and persistence of personality, factors which have typically been explored in captive animals, experimentally or in the absence of detailed behavioural observations in a social complex species. Using the multi-method approach described in this study, animal personality research can begin to build more comprehensive characterisations of personality to aid our understanding of taxonomic variation in personality structure. Using the Barbary macaque personality structure identified in this study, future researchers can now explore how different personality constructs affect ecological processes in wild Barbary macaques. For example, Barbary macaques appear to socialise with conspecifics which are similarly “excitable” to themselves. What effect does this have on social information or disease transfer? Are individuals in the “excitable” subset more likely to influence group movement and direction compared to their more conspecifics? Are any of the personality constructs related to fitness outcomes such as reproductive success or health? Once multiple personality constructs have been quantified in a species, as has been achieved in this thesis with Barbary macaques, researchers have the opportunity to explore more specific hypotheses about personality’s proximate associations and functional outcomes. It is hoped that the results of this thesis encourage future research into the personality of Barbary macaques and other species.

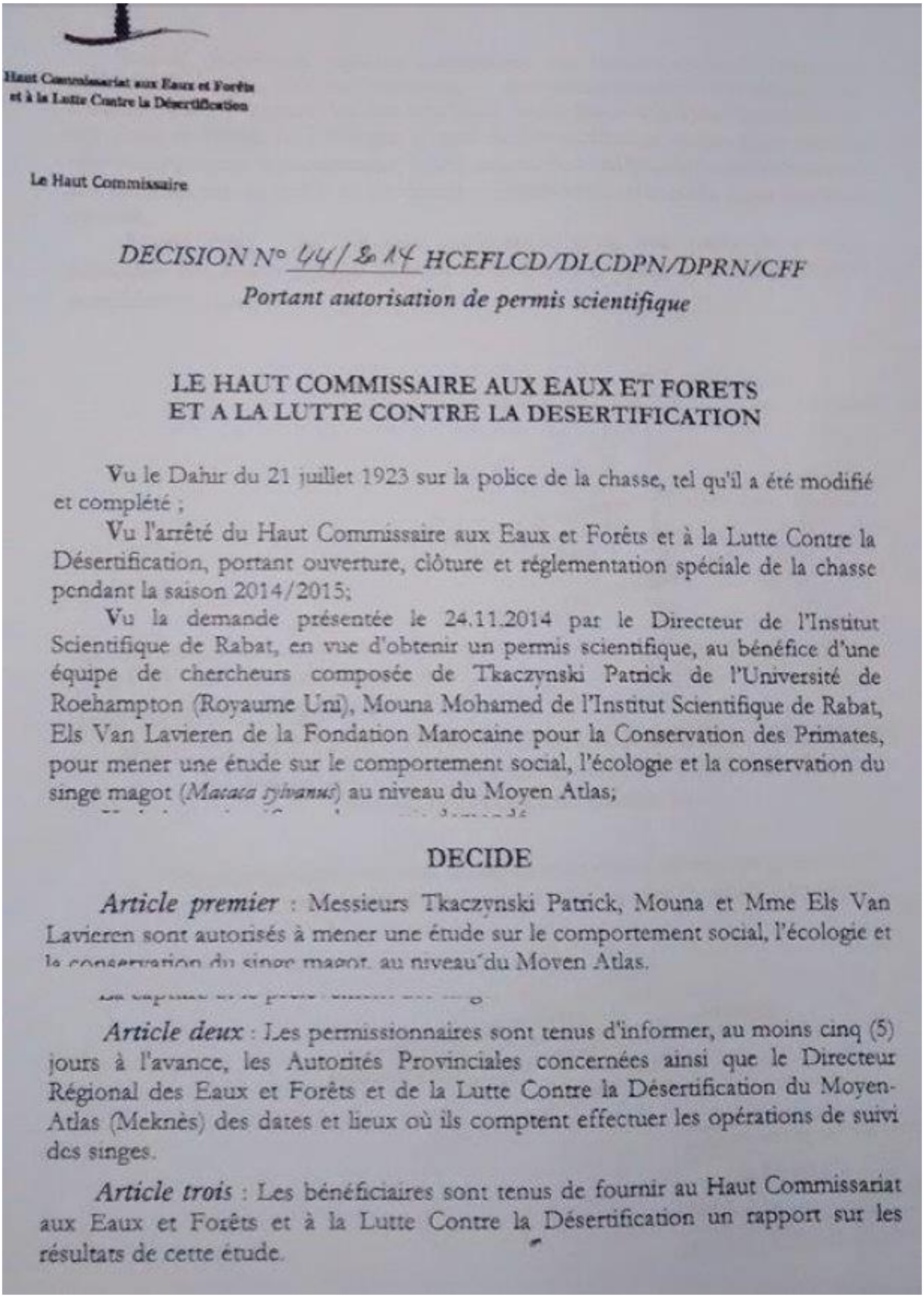
Appendices

A1 Ethics

The research for this project was submitted for ethics consideration under the reference LSC 13/ 088 in the Department of Life Sciences and was approved under the procedures of the University of Roehampton's Ethics Committee on 17.02.14.

A2 Permits

For the first field season, field work was carried out under the research permit provided to Dr Bonaventura Majolo (permit #253/2013; Barbary Macaque Project; University of Lincoln). For the second field season, the principal investigator secured their own research permit from the Haut-Commissariat aux Eaux et Forêts et à la Lutte Contre la Désertification, Royaume du Maroc. Photographs of this latter permit are below.



Haut Commissariat aux Eaux et Forêts
et à la Lutte Contre la Désertification

Le Haut Commissaire

DECISION N° 44/2014 HCEFLCD/DLCDPN/DPRN/CFF
Portant autorisation de permis scientifique

LE HAUT COMMISSAIRE AUX EAUX ET FORETS ET A LA LUTTE CONTRE LA DESERTIFICATION

Vu le Dahir du 21 juillet 1923 sur la police de la chasse, tel qu'il a été modifié et complété ;

Vu l'arrêté du Haut Commissaire aux Eaux et Forêts et à la Lutte Contre la Désertification, portant ouverture, clôture et réglementation spéciale de la chasse pendant la saison 2014/2015;

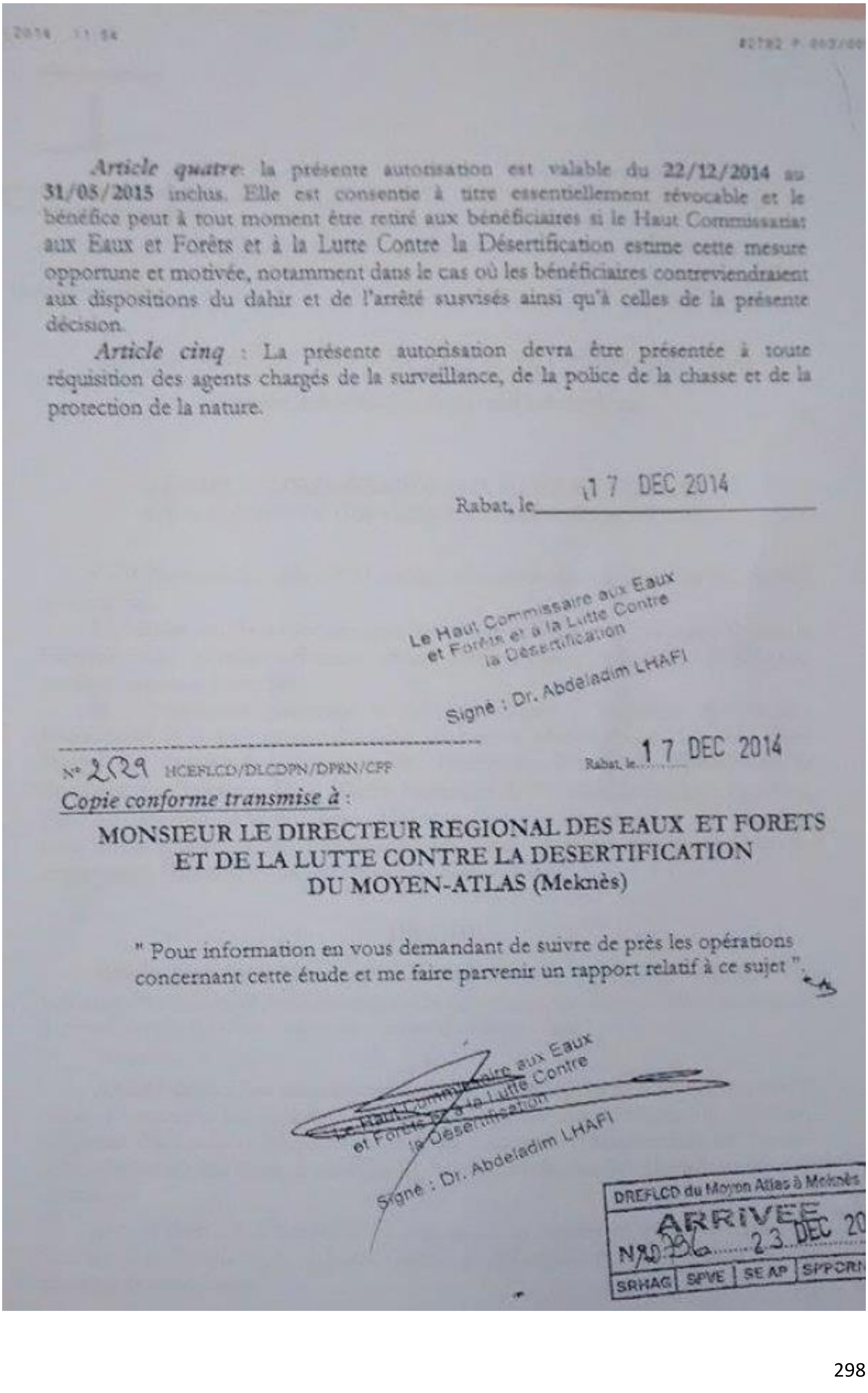
Vu la demande présentée le 24.11.2014 par le Directeur de l'Institut Scientifique de Rabat, en vue d'obtenir un permis scientifique, au bénéfice d'une équipe de chercheurs composée de Tkaczynski Patrick de l'Université de Roehampton (Royaume Uni), Mouna Mohamed de l'Institut Scientifique de Rabat, Els Van Lavieren de la Fondation Marocaine pour la Conservation des Primates, pour mener une étude sur le comportement social, l'écologie et la conservation du singe magot (*Macaca sylvanus*) au niveau du Moyen Atlas;

DECIDE

Article premier : Messieurs Tkaczynski Patrick, Mouna et Mme Els Van Lavieren sont autorisés à mener une étude sur le comportement social, l'écologie et la conservation du singe magot, au niveau du Moyen Atlas.

Article deux : Les permissionnaires sont tenus d'informer, au moins cinq (5) jours à l'avance, les Autorités Provinciales concernées ainsi que le Directeur Régional des Eaux et Forêts et de la Lutte Contre la Désertification du Moyen-Atlas (Meknès) des dates et lieux où ils comptent effectuer les opérations de suivi des singes.

Article trois : Les bénéficiaires sont tenus de fournir au Haut Commissariat aux Eaux et Forêts et à la Lutte Contre la Désertification un rapport sur les résultats de cette étude.



Article quatre : la présente autorisation est valable du **22/12/2014** au **31/05/2015** inclus. Elle est consentie à titre essentiellement révocable et le bénéfice peut à tout moment être retiré aux bénéficiaires si le Haut Commissariat aux Eaux et Forêts et à la Lutte Contre la Désertification estime cette mesure opportune et motivée, notamment dans le cas où les bénéficiaires contreviendraient aux dispositions du dahir et de l'arrêté susvisés ainsi qu'à celles de la présente décision.

Article cinq : La présente autorisation devra être présentée à toute réquisition des agents chargés de la surveillance, de la police de la chasse et de la protection de la nature.

Rabat, le 17 DEC 2014

Le Haut Commissaire aux Eaux
et Forêts et à la Lutte Contre
la Désertification

Signé : Dr. Abdeladim LHAFI

N° 2529 HCEFLCD/DLCDPN/DPRN/CPF

Rabat, le 17 DEC 2014

Copie conforme transmise à :

MONSIEUR LE DIRECTEUR REGIONAL DES EAUX ET FORETS
ET DE LA LUTTE CONTRE LA DESERTIFICATION
DU MOYEN-ATLAS (Meknès)

" Pour information en vous demandant de suivre de près les opérations concernant cette étude et me faire parvenir un rapport relatif à ce sujet ".

Le Haut Commissaire aux Eaux
et Forêts et à la Lutte Contre
la Désertification

Signé : Dr. Abdeladim LHAFI

A3 Ethograms

Ethogram of point events. Partners and/or direction were recorded where appropriate.

Behaviour definitions adapted from McFarland (2011).

Behaviour	Definition
Contact/Proximity Behaviours	
Approach 1m	Monkey approaches another monkey within 1m
Approach 5m	Monkey approaches another monkey within 5m
Depart 1m	Monkey leaves 1m proximity of another monkey
Depart 5m	Monkey leaves 5m proximity of another monkey
Supplant	Monkey is approached by another and creates a distance between itself and another monkey, by moving away from it, but not at full speed. Approaching monkey occupies vacated space
Embrace	Subject faces another monkey and they grab each other by the arms and/or feet
Genitals touch	Monkey touches another monkey’s genitals
Present for groom	Monkey presents a body part to be groomed by another monkey
Reciprocate grooming	Monkey goes from being groomed to immediately grooming partner, may be interspersed by a present to groom
Mock bite	Monkey softly bites another monkey (isolated, not part of sustained playing)
Touch body	Monkey touches with its hand another monkey, i.e. on the shoulder. The touch continues only for some seconds, but duration of the behaviour is not measured
Kiss	Monkey places its lips on another monkey’s lips
Submission	Monkey presents its hindquarters to another monkey as an indication of submission
Infant pick up	Infant not in contact with another monkey is picked up by subject
Sandwich	Infant is used as a “buffer” between the subject and another monkey, usually accompanied with an embrace and teeth chatter
Agonism-related Behaviours	
Aggress observer	Subject directs aggressive attention towards human observer
Lunge	Monkey makes a sudden intense movement towards another monkey; does not move a large distance
Charge	Monkey charges at another monkey for less than 5 metres
Chase	Monkey chases another monkey at high speed
Push & Pull	Monkey grabs hold of another monkey’s fur and skin and make shaking movement
Slap	Monkey hits another monkey with an opened hand
Jump on	Monkey jumps onto another
Bite	Monkey bites another monkey in the fur and skin
Checklook	During a conflict, subject looks over its shoulder, in a “ritualized” and “exaggerated” way, at a possible ally
Mount dominance	Subject mounts another monkey as an indication of dominance
Ground slap	Subject slaps ground with an opened hand in short, intense movements
Give aggression support	Subject joins another monkey in aggressing against a joint target, either by attacking or threatening the target
Receive aggression support	Subject is joined by another monkey in aggressing against a joint target, either by attacking or threatening the target
Give defence support	Subject gives support to another monkey which is being attacked, either by the positioning itself between the attacker and the monkey it is supporting or by threatening or attacking the original aggressor

Receive defence support	Subject gains support when being aggressed against, either by the supporting monkey positioning itself between the subject and the aggressing monkey or by threatening or attacking the monkey aggressing against the subject

Sexual Behaviours	
Present sex	Monkey turns it its hindquarters towards another monkey. When it does this, it exposes its genital region. This behaviour is usually followed by another sexual behaviour, such as inspect
Inspect sex	Monkey either sniffs or visually inspects the hindquarter of another monkey. This behaviour is often preceded or followed by other sexual elements, such as presenting or mounting
Sex dance	Male monkey stands bipedally (only on his hindlegs) and walks towards a female or passes by her towards her anogenital region. Often precedes copulation
Refuse sex	Active behaviour by monkey to prevent a sexual interaction with another monkey. These behaviours can include sitting down during a mount, or pushing away a presenting monkey
Reach or look back	Monkey reaches back and touches the leg of the monkey mounting it. This behaviour is often accompanied by a look-back by the subject
Start copulation	Male mounts female monkey and clasps its feet around the partners upper legs, while holding the partners hips with its hands. Pelvic thrusts have to be seen as well as intromission
Finishes copulation end	The copulation is ended, the male dismounts the female, AND signs of ejaculation can be seen (=pre-ejaculatory pause (i.e. male stiffens and then experience slight tremor), sperm on female or male genitalia or male genital self-grooming)
Unfinished copulation end	The copulation is ended, the male dismounts the female, NO signs of ejaculation can be seen

Solitary Behaviours	
Tree shake	Subject jumps on a branch, grasps it with both its hands and feet and shakes it
Masturbate	Subject touches its genital region over a prolonged time
Self-scratching	Subject scratches its own body, usually for no more than 2-3 seconds. Distinguish two different scratching events if they are separated by ≥ 10 seconds
Yawn	Subject yawns
Body shake	Subject shakes its fur like a dog
Gaze	Subject looks up from activity (e.g. feeding or grooming) and quickly scans around itself

Facial Displays	
Stare	The body of the monkey is tense; usually the head is lowered and stuck forward. Usually the animal has its hair standing up. The eyes are wide open; it stares at another monkey it is angry with. The ears are held out away from the head, sometimes the eyebrows are lifted
Open mouth	Body of the subject is tense, as described above. The monkey’s mouth is opened, the jaws are tensed, and the lips cover the teeth
Bared teeth	Subject pulls up its eyebrows and scalp, and flattens its ears against the head. The monkey pulls up its lips and shows its teeth and usually also its gums
Teeth chatter	Teeth bared as above. The monkey also opens and closes its mouth rapidly, sometimes with the tongue sticking out
Lipsmack	Subject looks at another monkey, the eyebrows and the scalp are often pulled up, and the ears are flattened against the head. The monkey opens and closes its mouth rapidly and repetitively, but the lips cover its teeth
Lift	Subject looks at another monkey repeatedly raising eyebrows. The ears are flattened against the head

Vocalisations	
Grunt	Subject makes a singular, low-pitched grunting sound

Fear scream	Subject produces a long, high-pitched scream when being submissive or attacked
Aggression scream	Subject produces a long, high-pitched scream when attacking another monkey
Pant	Subject makes low-pitched panting noises
Copulation calls	Various calls and grunts made when copulating
Long call	Loud vocalisation, usually to communicate long distances, i.e. when subject is lost or is searching for a missing member
Anthropogenic interactions	
Berber threat	Berber shepherd, farmer or stall owner threatens to attack subject or vice versa; no contact aggression is observed
Berber attack	Berber shepherd, farmer or stall owner physically attacks subject or vice versa
Tourist threat	Tourist threatens to attack subject or vice versa; no contact aggression is observed
Tourist attack	Tourist physically attacks subject or vice versa
Berber provision	Berber shepherd, farmer or stall owner feeds subject
Tourist provision	Tourist feeds subject
Begging	The monkey pulls trousers of tourist or berber, holds hand out for food or otherwise appears to be begging for food

A4 Barbary Macaque Personality Questionnaire

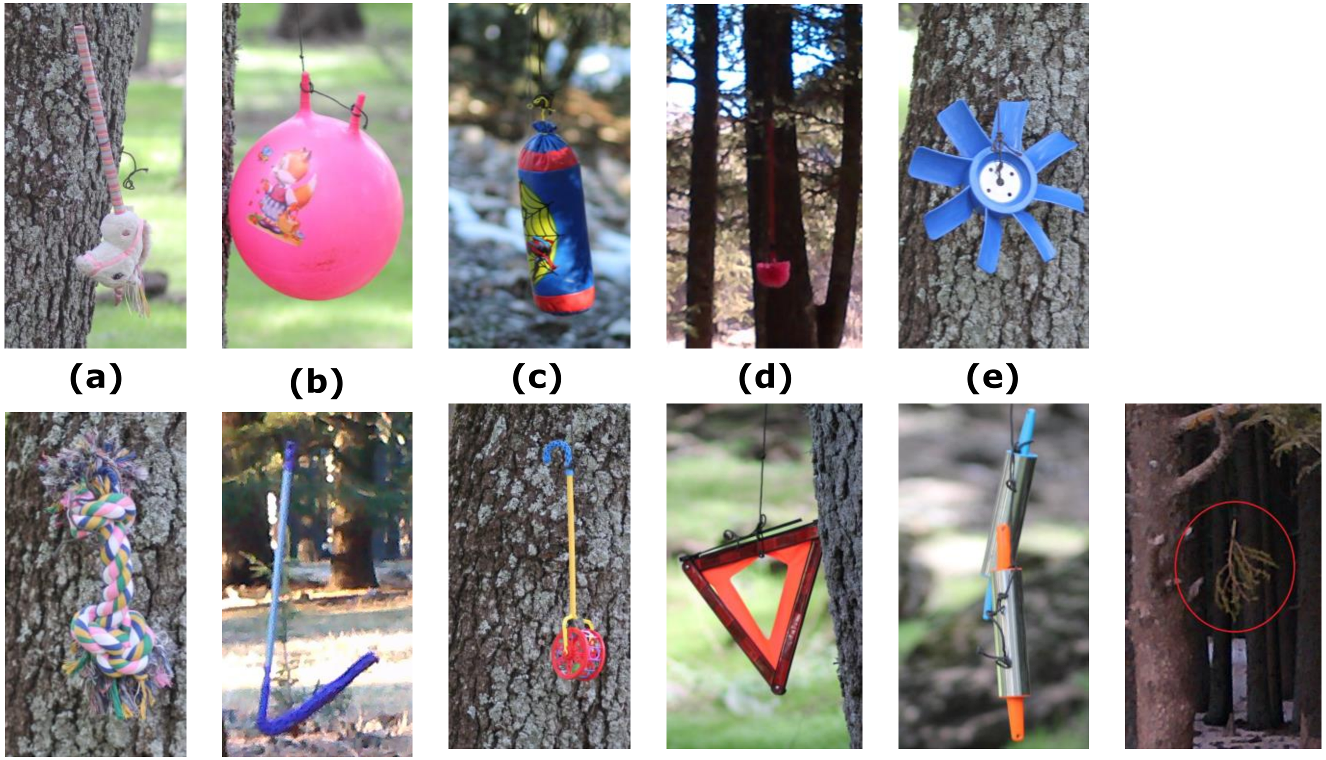
Actual questionnaire was provided in an excel sheet, with a column for ratings for each subject. Raters were asked to score on a 7 point scale (1 = the trait is absent in the subject; 7 = the subject exhibits extreme amounts of the trait) each subject on the relative presence or absence of each trait. Definitions adapted from Konečná et al, 2012.

Trait	Definition	Subject Rating
Active	Monkey seeks physical activity, and is fast and agile	
Intelligent	Monkey is quick and accurate in judging, comprehending both social and non-social situations and is successful in solving problems	
Fearful	Monkey reacts excessively to real or imagined threats, and is frightened by various stimuli	
Dominant	Monkey easily gets its own way, is able to control others and decisively intervenes in social interactions	
Cautious	Monkey avoids risky behaviors and situations	
Curious	Monkey seeks new objects and stimuli in the environment. It is interested in objects and the affairs of other monkeys that do not necessarily directly concern itself	
Playful	Monkey is eager to initiate play and joins in when play is solicited	
Assertive	Monkey is assertive or contentious in a way inconsistent with the usual dominance order. Monkey partly refuses the subordination relevant to its rank	
Erratic	Monkey’s behavior is unstable and unclear. Monkey changes mood very often	
Protective	Monkey tries to prevent harm or possible harm to others	
Impulsive	Monkey often displays some spontaneous or sudden behavior that could not have been anticipated. There often seems to be some emotional reason behind the sudden behavior	
Stingey	Monkey is excessively desirous of food, favored locations, or other resources in the enclose and is unwilling to share these resources with others	
Exploratory	Monkey is seeking new objects in its environment and seems to be eager to learn about them as much as possible	

Gentle	Monkey responds to others in an easy, kind manner
Confident	Monkey behaves in an assured manner, makes quick decisions about its reactions and does not hesitate
Tense	Monkey is restrained in movement and behavior, has difficulties relaxing in both social and non-social situations
Lazy	Monkey has inexpressive reactions, is inactive and slow
Manipulative	Monkey 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
Affectionate	Monkey has a warm attachment or closeness with others. Monkey’s behavior expresses the positive relationship to others
Conventional	Monkey seems to lack spontaneity or originality. Monkey behaves in a consistent manner from day to day and stays well within the social rules of the group
Independent	Monkey is individualistic and determines its own course of action without control or interference from other
Socially playful	Monkey engages in playful behavior preferably in social context. Solitary play is rare
Helpful	Monkey is willing to assist, accommodate, or cooperate with other monkeys
Timid	Monkey lacks self-confidence, is easily alarmed and is hesitant to venture into new social or non-social situations
Insecure	Monkey often relies on other monkeys for leadership, reassurance, and their support in social interactions
Inventive	Monkey is more likely than others to do new things including novel social or non-social behaviors. It tries new ways and approaches to reach its goal
Aggressive	Monkey often initiates physical fights or conflicts with others, it causes harm
Submissive	Monkey often gives in or yields to another monkey and doesn’t defend its own interests
Eccentric	Monkey shows unusual behaviors, which may include stereotypies or unusual mannerisms, or behavior that seems “crazy”
Opportunistic	Monkeys seizes a chance as soon as it arises in all types of situations
Irritable	Monkey is easily provoked to anger and exasperation; it is impatient and reacts in a negative manner even on mild provocations
Friendly	Monkey often seeks out amiable contact with others. Monkey infrequently initiates hostile behaviors towards others
Consistent	Monkey’s behavior is consistent and steady over extended periods of time. Monkey does little that is unexpected or deviates from its usual behavioral routine

Excitable	Monkey is easily aroused to an emotional state (can be positive or negative). Monkey becomes highly aroused by situations that would cause less arousal in most monkeys
Disorgranised	Monkey is scatterbrained and unpredictable in its behavior as if not following a consistent goal
Reckless	Monkey is unconcerned about the consequences of its behaviors. Only rarely is any distraction observed
Solitary	Monkey prefers to spend considerable time alone not seeking or even directly avoiding contact with others
Popular	Monkey is often sought out as a companion by others
Depressed	Monkey often appears isolated, withdrawn, sullen, brooding, and has reduced activity
Sympathetic	Monkey seems to be considerate and kind towards others as if sharing their feelings or trying to provide reassurance
Equable	Monkey reacts to its environment including the behavior of others in a calm, equable, way. Monkey is not easily upset by the behaviors of others
Permissive	Monkey reacts in balanced manner and does not necessarily reciprocate negative reactions. Monkey is more tolerant to behavior of others especially of younger or subordinate individuals
Jealous	Monkey is often troubled by others who are in a desirable or advantageous situation (such as having food, a choice location, or access to social partner). Subject may attempt to disrupt activities of advantaged monkeys
Alert	Monkey pays attention to other monkeys' behavior and its environment. Monkey does not seem to be tense; it is keeping an eye on the general situation
Patient	Monkey tends to follow the actions from start to finish, it does not oppose disturbance by others, but it may continue with the actions after the disturbance is over
Unemotional	Monkey is relatively placid and unlikely to become aroused, upset, happy, or sad
Selective	Monkeys tries to select the best food or place if having chance to do so, seems picky
Sensitive	Monkey is able to understand or read the mood, disposition, feelings, or intentions of others often on the basis of subtle, minimal cues and reacts accordingly
Persistent	Monkey tends to continue in a course of action, task, or strategy for a long time or continues despite opposition from others
Bullying	Monkey is overbearing and intimidating often without any provocation especially towards younger or lower ranking monkeys
Sociable	Monkey seeks, enjoys and keeps the company of other monkeys

A5 Objects for Exploration Assays

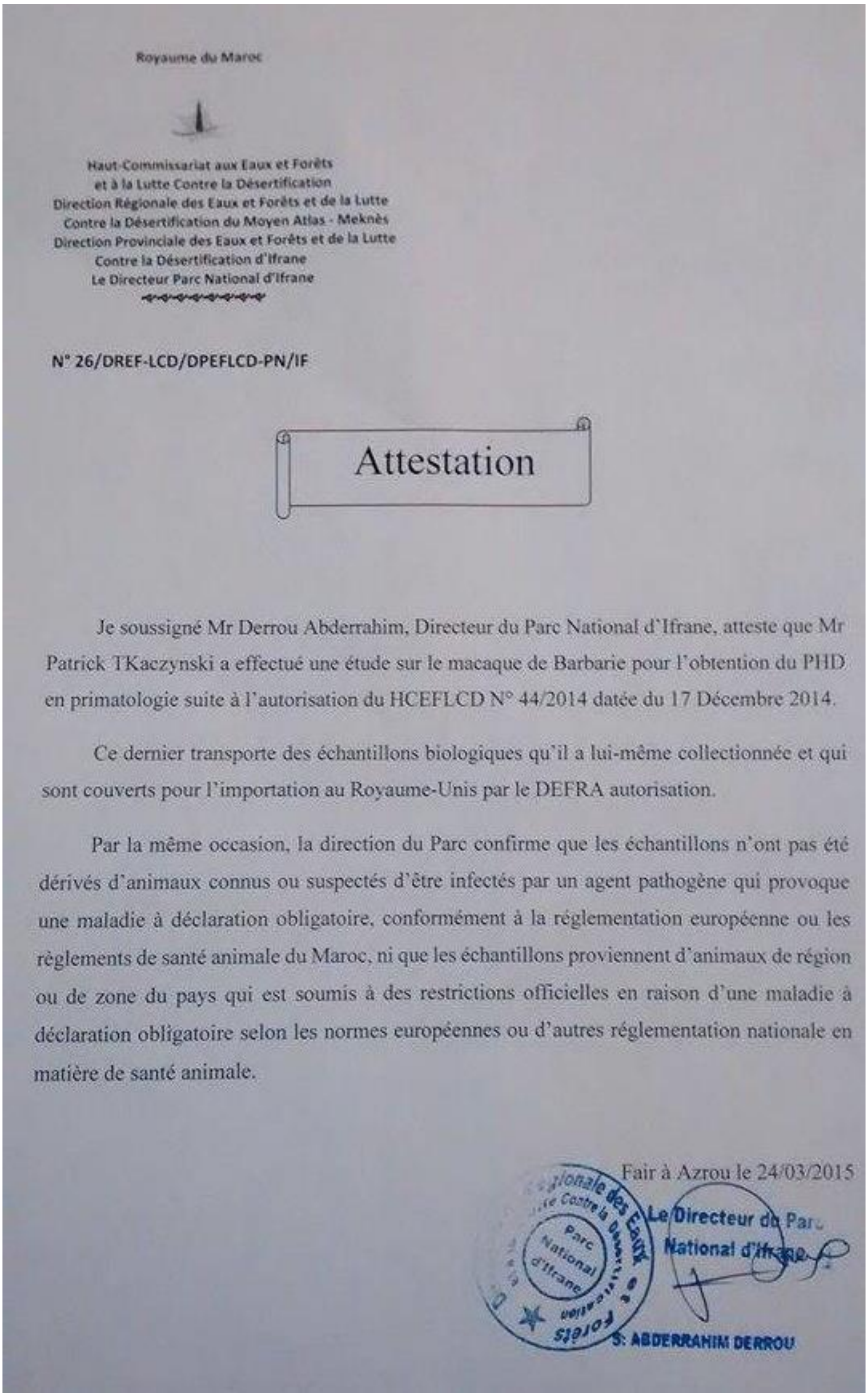


(a) (b) (c) (d) (e)

(f) (g) (h) (i) (j) (k)

The objects in pictures (a)-(j) were “treatments” in the novel object experiments used to quantify Exploration. Picture (k) shows how branches were suspended from tree (circled in red) for the “controls” of these novel object experiments. A different branch was used for each experiment. All objects (treatments and controls) were suspended from trees with brown rope.

A6 Attestation of subject health



Royaume du Maroc

Haut-Commissariat aux Eaux et Forêts
et à la Lutte Contre la Désertification
Direction Régionale des Eaux et Forêts et de la Lutte
Contre la Désertification du Moyen Atlas - Meknès
Direction Provinciale des Eaux et Forêts et de la Lutte
Contre la Désertification d'Ifrane
Le Directeur Parc National d'Ifrane

N° 26/DREF-LCD/DPEFLCD-PN/IF

Attestation

Je soussigné Mr Derrou Abderrahim, Directeur du Parc National d'Ifrane, atteste que Mr Patrick TKaczynski a effectué une étude sur le macaque de Barbarie pour l'obtention du PHD en primatologie suite à l'autorisation du HCEFLCD N° 44/2014 datée du 17 Décembre 2014.

Ce dernier transporte des échantillons biologiques qu'il a lui-même collectionnée et qui sont couverts pour l'importation au Royaume-Unis par le DEFRA autorisation.

Par la même occasion, la direction du Parc confirme que les échantillons n'ont pas été dérivés d'animaux connus ou suspectés d'être infectés par un agent pathogène qui provoque une maladie à déclaration obligatoire, conformément à la réglementation européenne ou les règlements de santé animale du Maroc, ni que les échantillons proviennent d'animaux de région ou de zone du pays qui est soumis à des restrictions officielles en raison d'une maladie à déclaration obligatoire selon les normes européennes ou d'autres réglementation nationale en matière de santé animale.

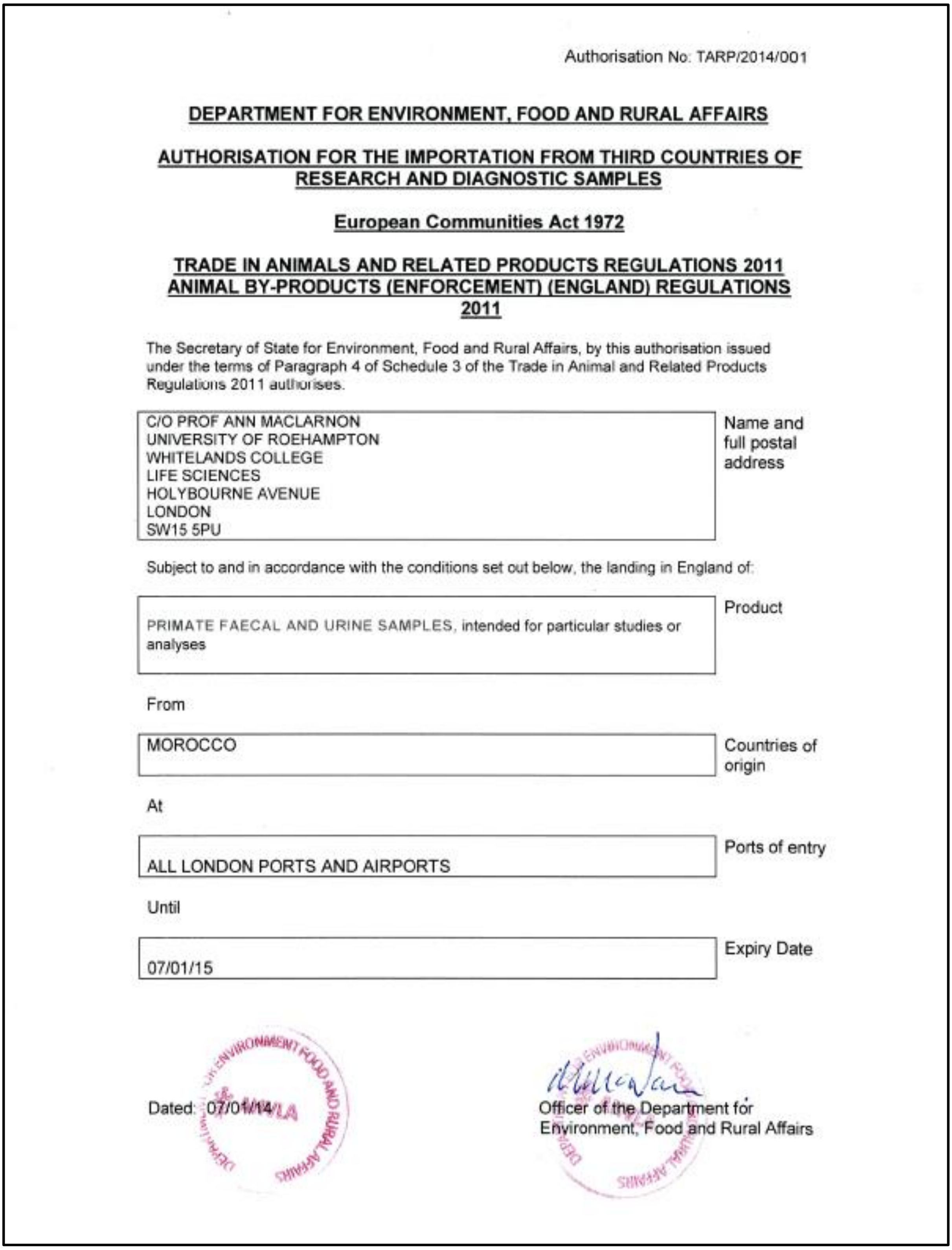
Fair à Azrou le 24/03/2015

Le Directeur du Parc
National d'Ifrane

S: ABDERRAHIM DERROU

A7 DEFRA Import Licences

2013/2014



Authorisation No: TARP/2014/001

DEPARTMENT FOR ENVIRONMENT, FOOD AND RURAL AFFAIRS

AUTHORISATION FOR THE IMPORTATION FROM THIRD COUNTRIES OF RESEARCH AND DIAGNOSTIC SAMPLES

European Communities Act 1972

TRADE IN ANIMALS AND RELATED PRODUCTS REGULATIONS 2011
ANIMAL BY-PRODUCTS (ENFORCEMENT) (ENGLAND) REGULATIONS 2011

The Secretary of State for Environment, Food and Rural Affairs, by this authorisation issued under the terms of Paragraph 4 of Schedule 3 of the Trade in Animal and Related Products Regulations 2011 authorises.

Name and full postal address:
C/O PROF ANN MACLARNON
UNIVERSITY OF ROEHAMPTON
WHITELANDS COLLEGE
LIFE SCIENCES
HOLYBOURNE AVENUE
LONDON
SW15 5PU

Subject to and in accordance with the conditions set out below, the landing in England of:

Product: PRIMATE FAECAL AND URINE SAMPLES, intended for particular studies or analyses

From

Countries of origin: MOROCCO

At

Ports of entry: ALL LONDON PORTS AND AIRPORTS

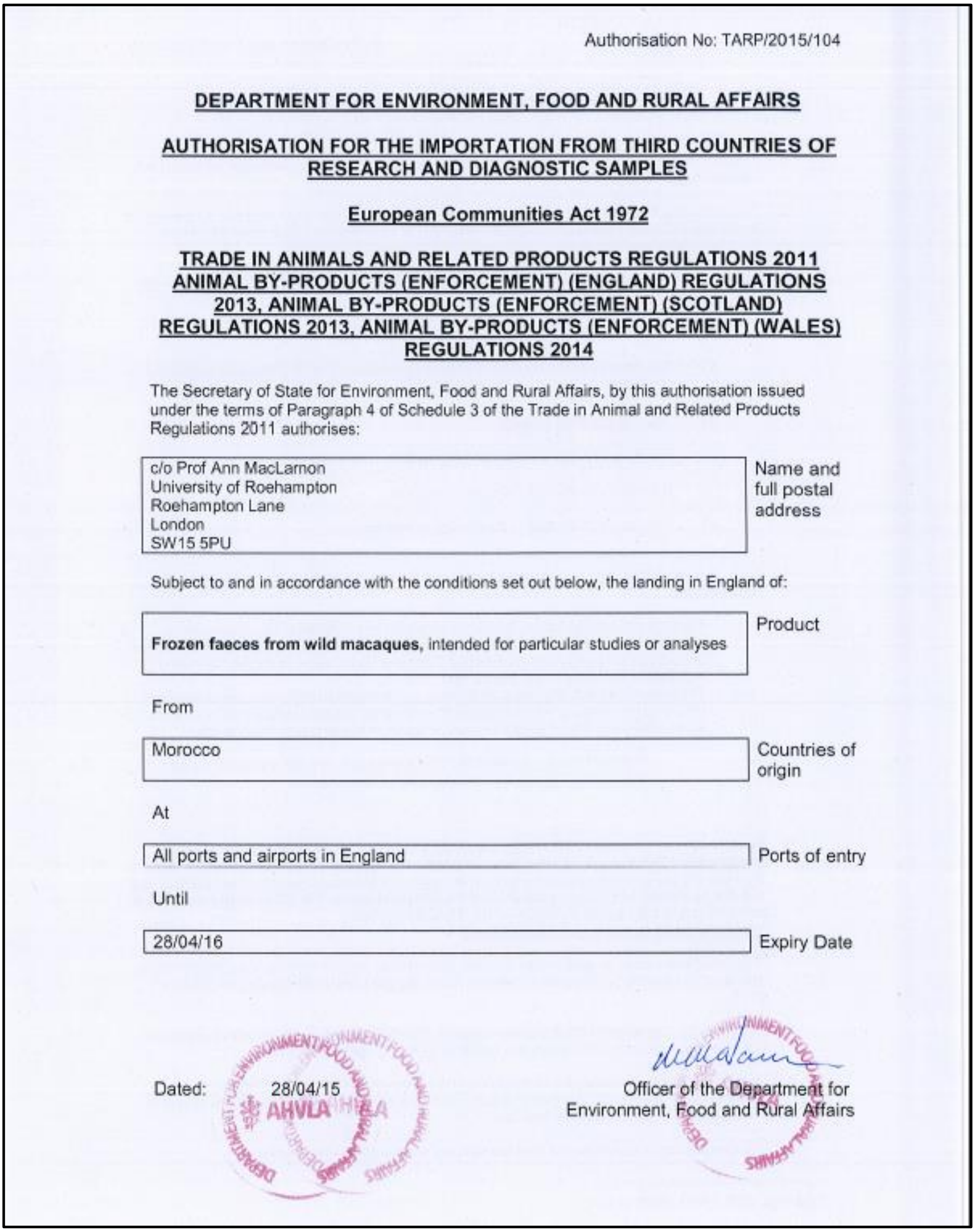
Until

Expiry Date: 07/01/15

Dated: 07/01/14

Officer of the Department for Environment, Food and Rural Affairs

2015



Authorisation No: TARP/2015/104

DEPARTMENT FOR ENVIRONMENT, FOOD AND RURAL AFFAIRS

AUTHORISATION FOR THE IMPORTATION FROM THIRD COUNTRIES OF RESEARCH AND DIAGNOSTIC SAMPLES

European Communities Act 1972

TRADE IN ANIMALS AND RELATED PRODUCTS REGULATIONS 2011 ANIMAL BY-PRODUCTS (ENFORCEMENT) (ENGLAND) REGULATIONS 2013, ANIMAL BY-PRODUCTS (ENFORCEMENT) (SCOTLAND) REGULATIONS 2013, ANIMAL BY-PRODUCTS (ENFORCEMENT) (WALES) REGULATIONS 2014

The Secretary of State for Environment, Food and Rural Affairs, by this authorisation issued under the terms of Paragraph 4 of Schedule 3 of the Trade in Animal and Related Products Regulations 2011 authorises:

c/o Prof Ann MacLarnon University of Roehampton Roehampton Lane London SW15 5PU	Name and full postal address

Subject to and in accordance with the conditions set out below, the landing in England of:

Frozen faeces from wild macaques, intended for particular studies or analyses	Product

From

Morocco	Countries of origin

At

All ports and airports in England	Ports of entry

Until

28/04/16	Expiry Date

Dated: 28/04/15

AHVLA

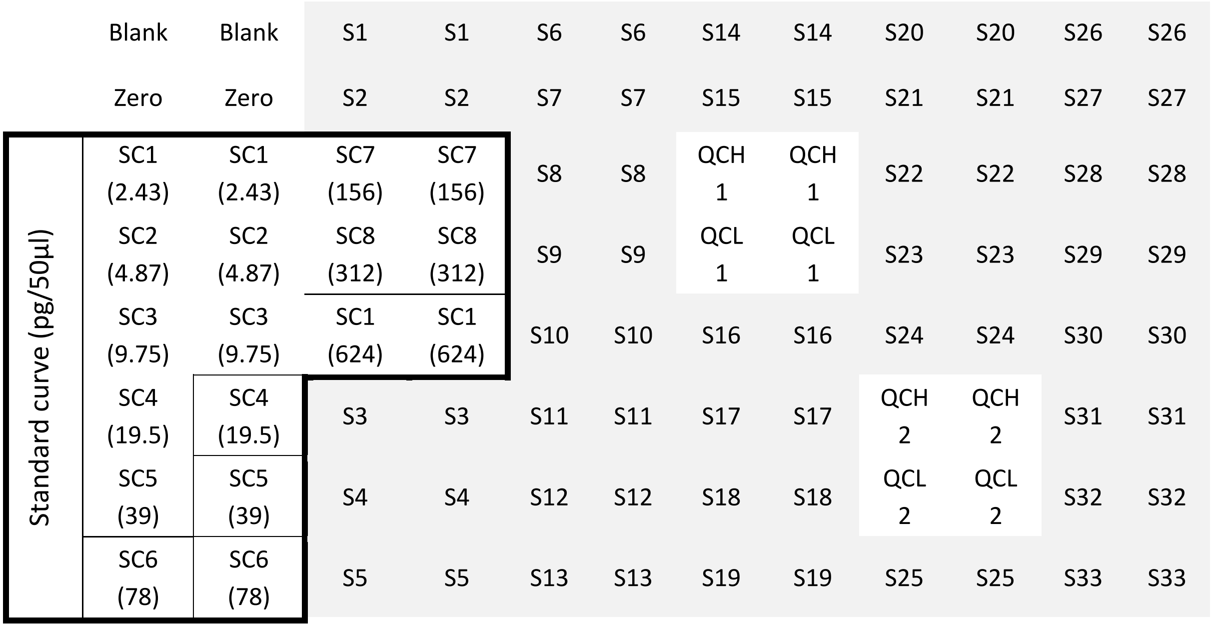
Officer of the Department for
Environment, Food and Rural Affairs

A8 Enzyme Immunoassay Plate Protocols and Layouts

EIA plates consisted of 48 duplicate 50µl wells. Blanks, zeros, standard curve, samples and quality controls (QCs) were pipetted into the appropriate wells. Biotin-labelled antigen is added to all wells bar the blanks and the plate is incubated overnight at 4°C (table A8 lists concentrations of reagents used). Unbound antigen is washed away and streptavidin-horseradish peroxidise added, which binds to the biotin on labelled antigens. The addition of TMB (3, 3′, 5, 5′-Tetramethylbenzidine –Sigma Aldrich T 2885) to these enzyme-biotin-labelled antigens results in a blue colour. Sulphuric acid is added to end the reaction and enzyme binding. The addition of sulphuric acid turns the enzyme-biotin-labelled antigens yellow. The optical density (OD) of the final solution can then be determined using a spectrophotometer and Ascent software. Figure A8 illustrates the layout of the plates.

Table A8: Volumes of reagents added to all wells (50µL].

Reagent	Antibody	Label	Assay buffer	Standard/sample/QC
Blank	0	50	100	0
Zero	50	50	50	0
Standard curve	50	50	0	50
QCH/QCL	50	50	0	50
Samples	50	50	0	50



	Blank	Blank	S1	S1	S6	S6	S14	S14	S20	S20	S26	S26
	Zero	Zero	S2	S2	S7	S7	S15	S15	S21	S21	S27	S27
Standard curve (pg/50µl)	SC1 (2.43)	SC1 (2.43)	SC7 (156)	SC7 (156)	S8	S8	QCH 1	QCH 1	S22	S22	S28	S28
	SC2 (4.87)	SC2 (4.87)	SC8 (312)	SC8 (312)	S9	S9	QCL 1	QCL 1	S23	S23	S29	S29
	SC3 (9.75)	SC3 (9.75)	SC1 (624)	SC1 (624)	S10	S10	S16	S16	S24	S24	S30	S30
	SC4 (19.5)	SC4 (19.5)	S3	S3	S11	S11	S17	S17	QCH 2	QCH 2	S31	S31
	SC5 (39)	SC5 (39)	S4	S4	S12	S12	S18	S18	QCL 2	QCL 2	S32	S32
	SC6 (78)	SC6 (78)	S5	S5	S13	S13	S19	S19	S25	S25	S33	S33

Figure A8: Basic microtitre layout containing standard curve (SC) concentrations, blanks, zeroes and QC High [100pg/50µL]and QC low [25pg/50 µL). The remaining 33 duplicates contained samples (S1-S33).

A9 Variance Inflation Factors

Table A9a: Variance inflation factor values for predictor variables in models exploring relationship between personality expression and stress physiology variables (mean faecal glucocorticoid concentration [fGC] and a coefficient of variation in fGC [fGCcv]). Excitability, Sociability and Tactility were analysed using values from each time block, Confidence, Introversion, Boldness and Exploration were analysed with mean values for the whole study period.

Model	Predictor	VIF
Excitability/Sociability/Tactility ~ fGC + fGCcv + sex + group	fGC	1.69
	fGCcv	1.11
	Sex	2.17
	Group	1.67
Confidence/Introversion/Boldness/Exploration ~ fGC +fGCcv + sex + group	fGC	1.14
	fGCcv	1.13
	Sex	2.03
	Group	1.01

Table A9b: Variance inflation factor values for predictor variables in models exploring relationship between personality expression and life history variables (rank and age). Excitability, Sociability and Tactility were analysed using values from each time block, Confidence, Introversion, Boldness and Exploration were analysed with mean values for the whole study period.

Model	Predictor	VIF
Excitability/Sociability/Tactility ~ rank + age + sex + group	Rank	1.01
	Age	1.14
	Sex	2.10
	Group	1.03
Confidence/Introversion/Boldness/Exploration ~ rank + age + group	Rank	1.04
	Age	1.18
	Sex	2.11
	Group	1.03

Table A9c: Variance inflation factor values for predictor variables in models exploring relationship between social network metrics and personality expression.

Model	Predictor	VIF
Social network metric ~ Excitability + rank + age + sex + group	Excitability	2.41
	Rank	1.09
	Age	1.20
	Sex	2.59
Social network metric ~ Sociability + rank + age + sex + group	Sociability	1.34
	Rank	1.38
	Age	1.13
	Sex	1.10
Social network metric ~ Tactility + rank + age + sex + group	Tactility	2.61
	Rank	1.07
	Age	1.47
	Sex	1.99
Social network metric ~ Confidence + rank + age + sex + group	Confidence	1.16
	Rank	1.10
	Age	1.20
	Sex	1.12
Social network metric ~ Introversion + rank + age + sex + group	Introversion	1.40
	Rank	1.35
	Age	1.07
	Sex	1.17
Social network metric ~ Boldness + rank + age + sex + group	Boldness	1.12
	Rank	1.10
	Age	1.05
	Sex	1.22
Social network metric ~ Exploration + rank + age + sex + group	Exploration	1.06
	Rank	1.06
	Age	1.13
	Sex	1.13

A10 Unreported Models

Table A10a: Best fit models used to describe relationship between male (a) Sociability, (b) Confidence, (c) Introversion, (d) Boldness and (e) Exploration scores and stress measures (fGC concentration and fGCcv). All models reported here did not differ significantly from a null (intercept only model).

Males (a)				
Full model	*Sociability ~ fGC + fGCcv + (subjects nested in group as random effect)*			
Best fit model	*β*	SE	Wald	*p*
Intercept	0.66	0.26	98.59	<0.01
fGC	<-0.01	<0.01	0.27	0.61
fGCcv	<0.01	<0.01	0.12	0.74
(b)				
Full model	*Confidence ~ fGC + fGCcv + group + fGC*group + fGCcv*group*			
Best fit model	*β*	SE	Wald	*p*
Intercept	3.50	0.50	-	-
Group	0.26	0.30	0.74	0.41
(c)				
Full model	*Introversion ~ fGC + fGCcv + group + fGC*group + fGCcv*group*			
Best fit model	*β*	SE	Wald	*p*
Intercept	-6.18	4.55	-	-
fGC	0.01	<0.01	0.45	0.52
fGCcv	0.05	0.04	0.03	0.88
Group	6.19	2.85	2.68	0.15
fGC*Group	<-0.01	<0.01	6.34	0.04
(d)				
Full model	*Boldness ~ fGC + fGCcv + group + fGC*group + fGCcv*group*			
Best fit model	*β*	SE	Wald	*p*
Intercept	-1.42	1.77	-	-
fGC	<0.01	<0.01	0.83	0.39
fGCcv	0.02	0.02	0.86	0.38
Group	1.43	1.11	<0.01	0.96
fGC*Group	<-0.01	<0.01	1.70	0.23
(e)				
Full model	*Exploration ~ fGC + fGCcv + group + fGC*group + fGCcv*group*			
Best fit model	*β*	SE	Wald	*p*
Intercept	-1.69	1.13	-	-
fGC	<0.01	<0.01	0.08	0.78

fGCcv	0.02	0.01	3.35	0.11
Group	1.03	0.71	0.15	0.71
fGC*Group	<-0.01	<0.01	1.97	0.20

Table A10b: Best fit models used to describe relationship between female (a) Excitability, (b) Sociability, (c) Confidence, (d) Introversion and (e) Boldness scores and stress measures (fGC concentration and fGCcv). All models reported here did not differ significantly from a null (intercept only model).

Females (a)				
Full model	*Excitability ~ fGC + fGCcv + (subjects nested in group as random effect)*			
Best fit model	*β*	SE	Wald	*p*
Intercept	1.37	1.22	41.91	<0.01
fGC	<0.01	<0.01	1.47	0.24
(b)				
Full model	*Sociability ~ fGC + fGCcv + (subjects nested in group as random effect)*			
Best fit model	*β*	SE	Wald	*p*
Intercept	4.39	0.96	182.38	<0.01
fGC	<0.01	<0.01	0.32	0.57
(c)				
Full model	*Confidence ~ fGC + fGCcv + group + fGC*group + fGCcv*group*			
Best fit model	*β*	SE	Wald	*p*
Intercept	4.47	1.02	-	-
fGC	<-0.01	<0.01	0.77	0.40
(d)				
Full model	*Introversion ~ fGC + fGCcv + group + fGC*group + fGCcv*group*			
Best fit model	*β*	SE	Wald	*p*
Intercept	2.14	0.80	-	-
Group	0.22	0.50	0.19	0.67
(e)				
Full model	*Boldness ~ fGC + fGCcv + group + fGC*group + fGCcv*group*			
Best fit model	*β*	SE	Wald	*p*
Intercept	1.31	1.55	-	-
fGC	<0.01	<0.01	0.55	0.48
fGCcv	-0.09	0.05	0.24	0.64
Group	-0.19	0.99	2.84	0.13

fGC*Group	<-0.01	<0.01	1.69	0.23
fGCcv*Group	0.06	0.04	3.01	0.12

Table A10c: Best fit models used to describe relationship between male (a) Sociability, (b) Confidence, (c) Introversion, (d) Boldness and (e) Exploration scores and life history measures (rank and age). All models reported here did not differ significantly from a null (intercept only model).

Males (a)				
Full model	_Sociability ~ rank + age + rank*age + (subjects nested in group as random effect)_			
Best fit model	_β_	SE	Wald	_p_
Intercept	0.60	0.06	101.47	<0.01
Rank	0.02	0.04	0.24	0.63
(b)				
Full model	_Confidence ~ rank + age + group + rank*age + rank*group + group+age_			
Best fit model	_β_	SE	Wald	_p_
Intercept	-1.20	2.73	-	-
Rank	-0.32	0.18	1.78	0.22
Age	2.13	1.22	0.60	0.46
Group	2.71	1.55	0.73	0.42
Age*Group	-1.111	0.68	2.62	0.15
(c)				
Full model	_Introversion ~ rank + age + group + rank*age + rank*group + group+age_			
Best fit model	_β_	SE	Wald	_p_
Intercept	-3.59	7.40	-	-
Rank	-1.24	1.50	2.21	0.19
Age	3.83	3.32	0.04	0.84
Group	3.90	4.11	2.09	0.20
Rank*Group	0.97	0.84	0.31	0.60
Age*Group	-2.15	1.83	1.37	0.29
(d)				
Full model	_Boldness ~ rank + age + group + rank*age + rank*group + group+age_			
Best fit model	_β_	SE	Wald	_p_
Intercept	2.53	1.41	-	-
Rank	-1.82	0.45	0.24	0.64
Age	-1.00	0.65	0.31	0.60

Group	-0.70	0.77	0.34	0.58
Rank*Age	0.79	0.20	14.79	0.01
Age*Group	0.41	0.34	1.40	0.28

(e)

Full model	*Exploration ~ rank + age + group + rank*age + rank*group + group+age*

Best fit model	*β*	SE	Wald	*p*
Intercept	0.32	0.33	-	-
Rank	-1.07	0.32	0.36	0.57
Age	-0.01	0.14	2.73	0.14
Group	0.13	0.10	0.31	0.59
Rank*Age	0.44	0.14	10.08	0.02

Table A10d: Best fit models used to describe relationship between female (a) Excitability, (b) Introversion, (c) Boldness and (d) Exploration and life history measures (rank and age). All models reported here did not differ significantly from a null (intercept only model).

Females
(a)

Full model	*Excitability ~ rank + age + rank*age + (subjects nested in group as random effect)*

Best fit model	*β*	SE	Wald	*p*
Intercept	2.75	0.43	41.03	<0.01
Rank	-0.11	0.33	0.11	0.74

(b)

Full model	*Introversion ~ rank + age + group + rank*age + rank*group + group+age*

Best fit model	*β*	SE	Wald	*p*
Intercept	-2.40	2.62	-	-
Rank	1.41	0.75	0.25	0.63
Age	2.11	1.24	1.14	0.31
Group	2.62	1.71	0.86	0.38
Rank*Group	-0.84	0.47	3.55	0.09
Age*Group	-1.13	0.87	1.67	0.23

(c)

Full model	*Boldness ~ rank + age + group + rank*age + rank*group + group+age*

Best fit model	*β*	SE	Wald	*p*
Intercept	1.19	0.38	-	-
Rank	-0.45	0.23	2.11	0.18

Age	-0.28	0.12	7.37	0.02
Group	0.14	0.14	1.19	0.30
Rank*Group	0.24	0.14	2.77	0.13

(d)

Full model	*Exploration ~ rank + age + group + rank*age + rank*group + group+age*			
Best fit model	*β*	SE	Wald	*p*
Intercept	0.80	0.32	-	-
Rank	1.41	0.48	2.33	0.16
Age	-0.08	0.11	0.14	0.72
Group	-0.09	0.12	0.90	0.37
Rank*Age	-0.40	0.17	2.01	0.19
Rank*Group	-0.32	0.13	6.07	0.04

Table A10e: Regression analyses of full models examining whether eigenvector centrality in grooming networks was related to (a) Excitability, (b) Sociability, (c) Tactility, (d) Confidence, (e) Introversion, (f) Boldness and (g) Exploration. Log likelihood ratio analyses are reported comparing full models to null models. Significant effects from regression analyses are in bold.

Grooming				
(a) Excitability	Full vs Null: F = 5.67, df = 6, p<0.01			
	β	SE	Wald	*p*
Intercept	1.36	1.89	-	-
Excitability	-0.12	0.29	3.17	0.09
Sex	**0.10**	**0.86**	**14.48**	**<0.01**
Rank	**-0.23**	**0.17**	**4.71**	**0.04**
Age	**-0.80**	**0.48**	**10.15**	**<0.01**
Excitability*Sex	0.17	0.14	1.45	0.24
Excitability*Age	-0.03	0.13	0.07	0.79
(b) Sociability	Full vs Null: F = 5.76, df = 6, p<0.01			
	β	SE	Wald	*p*
Intercept	1.10	2.36	-	-
Sociability	**-0.08**	**0.42**	**4.17**	**0.04**
Sex	**0.76**	**0.28**	**13.98**	**<0.01**
Rank	-0.78	0.71	3.37	0.08
Age	**-1.27**	**1.04**	**12.17**	**<0.01**
Sociability*Rank	0.12	0.14	0.71	0.41
Sociability*Age	0.08	0.19	0.19	0.67
(c) Tactility	Full vs Null: F = 5.57, df = 7, p<0.01			

	β	SE	Wald	*p*
Intercept	0.16	3.52	-	-
Tactility	**1.02**	**6.64**	**29.93**	**<0.01**
Sex	0.11	1.26	0.04	0.95
Rank	-0.71	0.56	3.23	0.09
Age	**-0.78**	**1.03**	**4.90**	**0.04**
Tactility*Sex	0.23	2.37	0.07	0.79
Tactility*Rank	0.73	0.84	0.81	0.38
Tactility*Age	0.35	1.66	0.04	0.84

(d) Confidence Full vs Null: F = 8.27, df = 6, p<0.01

	β	SE	Wald	*p*
Intercept	-5.21	2.62	-	-
Confidence	1.71	0.72	0.67	0.42
Sex	**0.83**	**0.25**	**19.43**	**<0.01**
Rank	**-0.56**	**0.61**	**7.36**	**0.01**
Age	**1.25**	**1.19**	**18.33**	**<0.01**
Confidence*Rank	0.08	0.15	0.07	0.79
Confidence*Age	-0.64	0.33	3.79	0.07

(e) Introversion Full vs Null: F = 10.56, df = 5, p<0.01

	β	SE	Wald	*p*
Intercept	0.66	1.49	-	-
Introversion	**0.06**	**0.39**	**31.29**	**<0.01**
Sex	1.21	0.79	3.49	0.08
Rank	**-0.24**	**0.13**	**4.98**	**0.04**
Age	**-0.75**	**0.23**	**11.80**	**<0.01**
Introversion*Sex	-0.27	0.24	1.22	0.28

(f) Boldness Full vs Null: F = 9.16, df = 4, p<0.01

	β	SE	Wald	*p*
Intercept	0.10	0.92	-	-
Boldness	**0.56**	**0.43**	**8.92**	**0.01**
Sex	**0.71**	**0.27**	**12.76**	**<0.01**
Rank	**-0.27**	**0.14**	**5.56**	**0.03**
Age	**-0.80**	**0.26**	**9.38**	**0.01**

(f) Exploration Full vs Null: F = 8.51, df = 4, p<0.01

	β	SE	Wald	*p*
Intercept	1.04	0.87	-	-
Exploration	-0.45	0.55	3.64	0.07
Sex	**0.68**	**0.28**	**12.00**	**0.01**
Age	**-0.27**	**0.14**	**6.33**	**0.02**
Rank	**0.90**	**0.26**	**12.06**	**<0.01**

Table A10f: Regression analyses of full models examining whether eigenvector centrality in co-feeding networks was related to (a) Excitability, (b) Sociability, (c) Tactility, (d) Confidence, (e) Introversion, (f) Boldness and (g) Exploration. Log likelihood ratio analyses are reported comparing full models to null models. Significant effects from regression analyses are in bold.

Co-feeding				
(a) Excitability	Full vs Null: F = 5.18, df = 6, p<0.01			
	β	SE	Wald	*p*
Intercept	2.48	1.94	-	-
Excitability	**-0.27**	**0.29**	**2.89**	**0.4**
Sex	-1.81	0.88	0.08	0.79
Rank	**-0.66**	**0.17**	**23.61**	**<0.01**
Age	0.22	0.50	0.09	0.77
Excitability*Sex	0.30	0.14	4.15	0.06
Excitability*Age	-0.07	0.12	0.28	0.61
(b) Sociability	Full vs Null: F = 12.02, df = 6, p<0.01			
	β	SE	Wald	*p*
Intercept	0.55	1.81	-	-
Sociability	**-0.04**	**0.32**	**56.01**	**<0.01**
Sex	-0.23	0.22	2.01	0.17
Rank	**-0.77**	**0.54**	**11.99**	**<0.01**
Age	-0.89	0.80	0.06	0.81
Sociability*Rank	0.06	0.10	0.41	0.53
Sociability*Age	0.18	0.41	1.64	0.21
(c) Tactility	Full vs Null: F = 5.32, df = 6, p<0.01			
	β	SE	Wald	*p*
Intercept	-4.12	3.57	-	-
Tactility	7.93	6.75	1.81	0.19
Sex	**-1.21**	**1.29**	**9.11**	**0.01**
Rank	**-1.37**	**0.57**	**21.41**	**<0.01**
Age	1.82	1.05	1.84	0.19
Tactility*Sex	0.10	2.41	0.01	0.94
Tactility*Rank	1.11	0.85	1.31	0.27
Tactility*Age	-2.23	1.69	1.75	0.20
(d) Confidence	Full vs Null: F = 4.32, df = 6, p<0.01			
	β	SE	Wald	*p*
Intercept	1.00	3.23	-	-
Confidence	**-0.25**	**0.89**	**4.77**	**0.04**
Sex	-0.22	0.31	0.54	0.47
Rank	**-1.26**	**0.75**	**19.56**	**<0.01**
Age	-0.72	1.46	<0.01	0.95
Confidence*Rank	0.14	0.19	0.76	0.39

Confidence*Age	0.22	0.41	0.30	0.59

(e) Introversion	Full vs Null: F = 10.32, df = 5, p<0.01			
	β	SE	Wald	*p*
Intercept	2.19	1.50	-	-
Introversion	**-0.54**	**0.39**	**12.84**	**<0.01**
Sex	**-0.86**	**0.79**	**12.63**	**<0.01**
Rank	**-0.64**	**0.13**	**24.99**	**<0.01**
Age	0.24	0.23	1.12	0.30
Introversion*Sex	0.05	0.25	0.04	0.84

(f) Boldness	Full vs Null: F = 6.20, df = 4, p<0.01			
	β	SE	Wald	*p*
Intercept	-0.13	1.03	-	-
Boldness	0.30	0.48	1.39	0.25
Sex	-0.27	0.30	1.62	0.22
Rank	**-0.72**	**0.16**	**21.58**	**<0.01**
Age	0.14	0.29	0.23	0.64

(f) Exploration	Full vs Null: F = 6.00, df = 4, p<0.01			
	β	SE	Wald	*p*
Intercept	0.21	0.96	-	-
Exploration	0.01	0.61	1.39	0.25
Sex	-0.27	0.31	1.62	0.22
Age	**-0.73**	**0.16**	**21.58**	**<0.01**
Rank	0.09	0.28	0.23	0.64

Table A10g: Regression analyses of full models examining whether eigenvector centrality in nearest neighbour networks was related to (a) Excitability, (b) Sociability, (c) Tactility, (d) Confidence, (e) Introversion, (f) Boldness and (g) Exploration. Log likelihood ratio analyses are reported comparing full models to null models. Significant effects from regression analyses are in bold.

Nearest neighbour				
(a) Excitability	Full vs Null: F = 5.08, df = 6, p<0.01			
	β	SE	Wald	*p*
Intercept	3.98	1.95	-	-
Excitability	-0.67	0.29	0.56	0.46
Sex	-1.85	0.89	1.37	0.26
Rank	**-0.64**	**0.17**	**18.98**	**<0.01**
Age	-0.42	0.50	0.12	0.73
Excitability*Sex	**041**	**0.14**	**9.25**	**0.01**
Excitability*Age	0.06	0.12	0.23	0.64

(b) Sociability	Full vs Null: F = 11.72, df = 6, p<0.01			
	β	SE	Wald	*p*
Intercept	-1.76	1.83	-	-
Sociability	**0.40**	**0.33**	**63.30**	**<0.01**
Sex	0.05	0.22	0.11	0.75
Rank	**-0.56**	**0.55**	**6.00**	**0.02**
Age	-0.24	0.81	0.54	0.47
Sociability*Rank	0.05	0.11	0.25	0.62
Sociability*Age	0.02	0.15	0.03	0.87

(c) Tactility	Full vs Null: F = 3.88, df = 6, p=0.01			
	β	SE	Wald	*p*
Intercept	-3.50	3.94	-	-
Tactility	**6.58**	**7.45**	**5.78**	**0.03**
Sex	**-1.53**	**1.42**	**4.68**	**0.04**
Rank	**-0.70**	**0.63**	**13.41**	**<0.01**
Age	1.76	1.16	0.63	0.44
Tactility*Sex	1.19	2.66	0.84	0.37
Tactility*Rank	0.20	0.94	0.01	0.97
Tactility*Age	-2.50	1.86	1.80	0.20

(d) Confidence	Full vs Null: F = 3.52, df = 6, p=0.02			
	β	SE	Wald	*p*
Intercept	-2.20	3.52	-	-
Confidence	**0.65**	**0.94**	**5.44**	**0.03**
Sex	0.13	0.33	0.29	0.59
Rank	**-1.44**	**0.79**	**13.65**	**<0.01**
Age	0.24	1.55	0.54	0.47
Confidence*Rank	0.21	0.20	1.07	0.31
Confidence*Age	-0.12	0.43	0.07	0.78

(e) Introversion	Full vs Null: F = 8.55, df = 5, p<0.01			
	β	SE	Wald	*p*
Intercept	1.11	1.60	-	-
Introversion	**-0.24**	**0.42**	**20.06**	**<0.01**
Sex	**0.13**	**0.85**	**5.26**	**0.03**
Rank	**-0.57**	**0.14**	**16.77**	**<0.01**
Age	0.10	0.25	0.10	0.77
Introversion*Sex	-0.20	0.26	0.58	0.46

(f) Boldness	Full vs Null: F = 4.49, df = 4, p=0.01			
	β	SE	Wald	*p*
Intercept	-0.53	1.11	-	-
Boldness	0.59	0.51	3.38	0.08
Sex	0.02	0.33	0.01	0.93
Rank	**-0.63**	**0.17**	**14.55**	**<0.01**
Age	<0.01	0.32	>0.01	>0.99

(f) Exploration	Full vs Null: F = 4.12, df = 4, p=0.01			
	β	SE	Wald	*P*
Intercept	0.45	1.04	-	-
Exploration	-0.46	0.67	1.76	0.20
Sex	-0.01	0.34	0.02	0.88
Age	**-0.64**	**0.17**	**14.61**	**<0.01**
Rank	-0.10	0.31	0.10	0.76

Table A10h: Regression analyses of full models examining whether individual clustering coefficient in grooming networks was related to (a) Excitability, (b) Sociability, (c) Tactility, (d) Confidence, (e) Introversion, (f) Boldness and (g) Exploration. Log likelihood ratio analyses are reported comparing full models to null models. Significant effects from regression analyses are in bold.

Grooming				
(a) Excitability	Full vs Null: F = 2.24, df = 6, p=0.08			
	β	SE	Wald	*p*
Intercept	1.95	2.40	-	-
Excitability	-0.73	0.36	1.19	0.29
Sex	-0.90	1.09	2.99	0.10
Rank	-0.30	0.21	0.25	0.62
Age	**-0.22**	**0.61**	**4.77**	**0.04**
Excitability*Sex	0.10	0.18	0.88	0.36
Excitability*Age	0.28	0.15	3.36	0.08
(b) Sociability	Full vs Null: F = 1.43, df = 6, p=0.25			
	β	SE	Wald	*p*
Intercept	1.19	3.26	-	-
Sociability	-0.41	0.58	1.19	0.29
Sex	-0.38	0.39	2.99	0.10
Rank	-0.12	0.98	0.25	0.62
Age	**-0.36**	**1.43**	**4.77**	**0.04**
Sociability*Rank	0.01	0.19	0.88	0.36
Sociability*Age	0.21	0.26	3.36	0.08
(c) Tactility	Full vs Null: F = 1.26, df = 6, p=0.32			
	β	SE	Wald	*p*
Intercept	-2.26	5.08	-	-
Tactility	2.01	9.60	2.20	0.15
Sex	-1.63	1.83	0.94	0.34
Rank	-0.40	0.81	0.13	0.72
Age	**1.87**	**1.50**	**4.64**	**0.04**
Tactility*Sex	1.56	3.43	0.37	0.55

Tactility*Rank	0.46	1.21	0.09	0.77
Tactility*Age	-1.56	2.40	0.42	0.52
(d) Confidence	Full vs Null: F = 1.92, df = 6, p=0.13			
	β	SE	Wald	*p*
Intercept	5.11	3.90	-	-
Confidence	-1.77	1.07	0.46	0.51
Sex	-0.44	0.38	3.01	0.10
Rank	-0.25	0.90	0.04	0.85
Age	**-2.02**	**1.76**	**5.15**	**0.03**
Confidence*Rank	0.03	0.23	0.15	0.70
Confidence*Age	0.81	0.49	2.72	0.11
(e) Introversion	Full vs Null: F = 2.32, df = 5, p=0.08			
	β	SE	Wald	*p*
Intercept	2.08	2.24	-	-
Introversion	-0.92	0.58	1.37	0.25
Sex	-2.23	1.18	2.23	0.15
Rank	-0.07	0.19	0.12	0.73
Age	**0.71**	**0.35**	**5.15**	**0.03**
Introversion*Sex	0.61	0.37	2.75	0.11
(f) Boldness	Full vs Null: F = 2.24, df = 4, p=0.10			
	β	SE	Wald	*p*
Intercept	-1.51	1.27	-	-
Boldness	0.43	0.58	0.01	0.97
Sex	-0.39	0.37	3.32	0.08
Rank	-0.11	0.19	0.06	0.81
Age	**0.85**	**0.36**	**5.58**	**0.03**
(f) Exploration	Full vs Null: F = 3.21, df = 4, p=0.03			
	β	SE	Wald	*p*
Intercept	-1.82	1.10	-	-
Exploration	**1.29**	**0.70**	**4.46**	**0.04**
Sex	-0.29	0.35	2.60	0.12
Age	-0.17	0.18	0.33	0.57
Rank	**0.77**	**0.33**	**5.47**	**0.03**

Table A10h: Regression analyses of full models examining whether individual clustering coefficient in co-feeding networks was related to (a) Excitability, (b) Sociability, (c) Tactility, (d) Confidence, (e) Introversion, (f) Boldness and (g) Exploration. Log likelihood ratio analyses are reported comparing full models to null models. Significant effects from regression analyses are in bold.

Co-feeding

(a) Excitability	Full vs Null: F = 0.99 df = 6, p=0.45			
	β	SE	Wald	*p*
Intercept	0.60	2.72	-	-
Excitability	-0.25	0.41	0.15	0.71
Sex	-0.05	1.24	0.18	0.68
Rank	**0.40**	**0.24**	**5.04**	**0.04**
Age	-0.38	0.70	0.01	0.93
Excitability*Sex	0.04	0.20	0.1	0.75
Excitability*Age	0.12	0.17	0.49	0.49

(b) Sociability	Full vs Null: F = 3.43, df = 6, p=0.02			
	β	SE	Wald	*p*
Intercept	-3.23	2.74	-	-
Sociability	0.80	0.49	2.88	0.10
Sex	-0.44	0.33	0.56	0.46
Rank	**2.88**	**0.82**	**4.73**	**0.04**
Age	1.57	1.20	0.01	0.98
Sociability*Rank	**-0.50**	**0.16**	**9.77**	**0.01**
Sociability*Age	-0.35	0.22	2.67	0.12

(c) Tactility	Full vs Null: F = 1.62, df = 6, p=0.19			
	β	SE	Wald	*p*
Intercept	2.71	4.86	-	-
Tactility	-4.59	9.18	0.16	0.71
Sex	-2.12	1.74	0.20	0.66
Rank	**1.49**	**0.77**	**6.05**	**0.02**
Age	0.23	1.43	0.09	0.75
Tactility*Sex	3.30	3.28	2.87	0.1
Tactility*Rank	-1.62	1.16	2.05	0.17
Tactility*Age	-0.40	2.29	0.03	0.86

(d) Confidence	Full vs Null: F = 1.954, df = 6, p=0.21			
	β	SE	Wald	*p*
Intercept	4.99	4.04	-	-
Confidence	-1.22	1.11	0.01	0.98
Sex	-0.32	0.39	0.37	0.55
Rank	**1.91**	**0.94**	**5.53**	**0.03**
Age	-2.22	1.83	0.02	0.90
Confidence*Rank	-0.36	0.24	1.99	0.18
Confidence*Age	0.60	0.51	1.36	0.26

(e) Introversion	Full vs Null: F = 1.32, df = 5, p=0.28			
	β	SE	Wald	*p*
Intercept	-1.83	2.43	-	-
Introversion	0.65	0.63	1.61	0.22
Sex	0.93	1.28	0.01	0.98
Rank	0.39	0.21	4.24	0.05
Age	-0.02	0.38	0.02	0.87

Introversion*Sex	-0.34	0.40	0.76	0.39

(f) Boldness	Full vs Null: F = 1.57, df = 4, p=0.22			
	β	SE	Wald	*p*
Intercept	1.02	1.33	-	-
Boldness	-0.52	0.61	1.46	0.24
Sex	-0.24	0.39	0.23	0.64
Rank	**0.43**	**0.20**	**4.53**	**0.04**
Age	-0.10	0.38	0.07	0.79

(f) Exploration	Full vs Null: F = 1.35, df = 4, p=0.28			
	β	SE	Wald	*p*
Intercept	0.37	1.24	-	-
Exploration	0.07	0.79	0.29	0.59
Sex	-0.24	0.40	0.24	0.63
Age	**0.44**	**0.20**	**4.88**	**0.04**
Rank	-0.01	0.37	<0.01	0.97

Table A10i: Regression analyses of full models examining whether individual clustering coefficient in nearest neighbour networks was related to (a) Excitability, (b) Sociability, (c) Tactility, (d) Confidence, (e) Introversion, (f) Boldness and (g) Exploration. Log likelihood ratio analyses are reported comparing full models to null models. Significant effects from regression analyses are in bold.

Nearest neighbour				
(a) Excitability	Full vs Null: F = 1.47, df = 6, p=0.45			
	β	SE	Wald	*p*
Intercept	6.59	2.58	-	-
Excitability	-0.55	0.39	1.25	0.28
Sex	-2.02	1.18	4.13	0.06
Rank	-0.13	0.23	0.24	0.63
Age	-0.97	0.66	2.58	0.12
Excitability*Sex	0.06	0.19	0.23	0.64
Excitability*Age	0.11	0.17	0.41	0.53

(b) Sociability	Full vs Null: F = 0.81, df = 6, p=0.58			
	β	SE	Wald	*P*
Intercept	6.56	3.50	-	-
Sociability	-1.04	0.62	0.03	0.87
Sex	-0.13	0.424	0.06	0.81
Rank	-0.71	1.05	0.07	0.80

Age	-2.88	1.54	0.86	0.36
Sociability*Rank	0.17	0.20	0.67	0.42
Sociability*Age	0.49	0.28	3.15	0.09

(c) Tactility	Full vs Null: F = 0.26, df = 6, p=0.96			
	β	SE	Wald	*P*
Intercept	5.72	5.87	-	-
Tactility	-8.79	11.10	0.04	0.84
Sex	-0.40	2.11	0.01	0.91
Rank	-0.06	0.94	0.01	0.91
Age	-1.88	1.73	0.95	0.34
Tactility*Sex	1.27	3.96	0.01	0.99
Tactility*Rank	0.10	1.40	0.03	0.85
Tactility*Age	2.39	2.77	0.75	0.40

(d) Confidence	Full vs Null: F = 0.71, df = 6, p=0.65			
	β	SE	Wald	*p*
Intercept	-1.98	4.45	-	-
Confidence	0.78	1.22	0.02	0.88
Sex	-0.09	0.43	0.05	0.83
Rank	-1.70	1.03	0.03	0.87
Age	0.71	2.01	0.93	0.35
Confidence*Rank	0.46	0.26	2.92	0.10
Confidence*Age	-0.28	0.55	0.25	0.62

(e) Introversion	Full vs Null: F = 0.66, df = 5, p=0.66			
	β	SE	Wald	*p*
Intercept	4.63	2.59	-	-
Introversion	-1.04	0.67	0.22	0.65
Sex	-2.19	1.37	0.28	0.60
Rank	0.14	0.22	0.09	0.77
Age	-0.38	0.40	0.62	0.44
Introversion*Sex	0.61	0.42	2.09	0.16

(f) Boldness	Full vs Null: F = 0.57, df = 4, p=0.69			
	β	SE	Wald	*p*
Intercept	0.17	1.43	-	-
Boldness	0.77	0.66	1.72	0.20
Sex	-0.22	0.42	0.13	0.72
Rank	0.09	0.22	0.13	0.72
Age	-0.22	0.41	0.29	0.29

(f) Exploration	Full vs Null: F = 0.22, df = 4, p=0.92			
	β	SE	Wald	*p*
Intercept	1.19	1.35	-	-
Exploration	-0.18	0.87	0.03	0.87
Sex	-0.22	0.44	0.07	0.79
Age	0.07	0.22	0.03	0.86
Rank	-0.35	0.40	0.76	0.39

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