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Comparative lower-order hierarchical personality structure and personality development in nonhuman great apes

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Declaration

I hereby declare that this thesis is of my own composition, and that it contains no material previously submitted for the award of any other degree. The work reported in this thesis has been executed by myself, except where due acknowledgement is made in the text.

(*Conor G. Smith*)

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A Note on Personal Pronouns

This thesis is based to a large extent on published work and work under review. In order to maintain consistency with the published literature, and to acknowledge the collaborative nature of the work, "we" rather than "I" is used throughout.

Lay Summary

Personality traits like extraversion and neuroticism are organised into a hierarchy of levels from the individual items of a questionnaire up to the factors themselves. Between these levels are facets, which make up different parts of the overall factor. These lower levels of structure can be used to provide a more detailed understanding of personality than the broader domains. While these levels have been used in human research, they have not been applied to non-human personality in a comprehensive way. Here we identify two lower-level structures of personality in chimpanzees, bonobos, orangutans, and gorillas. We then used the fine-grained item level to explore in more detail the way personality differs with age in these species. We also provide a summary of how this development can be contextualised in evolutionary history and set out a method for applying questionnaire based personality research to lemurs. Overall, this thesis provides an introduction of lower-order trait structure to the field of nonhuman personality and demonstrates the value of this addition through a new understanding of personality and ageing in great apes.

Abstract

The aim of this thesis is to identify the structure of personality below the factor level in chimpanzees, bonobos, orangutans, gorillas in terms of both facets and items and to investigate the development of these lower-order traits over the lifespan in these species. First, we aim to summarise the field of personality development in nonhuman animals at the factor level and exploring potential pathways and mechanisms that can explain how these different personality structures evolved in a wide variety of species. Next, we identify the facet structure of personality traits in four great apes using data-driven analytic methods and compare this structure amongst species. Third, we go beyond facets to the finer hierarchical level of nuances or items and explore how the greater detail available from using these levels of personality improve our understanding of how personality varies with age in the same four species. Finally, we lay out a method for the adaptation of these personality questionnaire instruments to identify personality structure in a new primate family, lemurs. These lower-order structures have great potential to increase understanding of personality in nonhuman animals and this thesis provides a solid foundation for wider adoption of these ideas.

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Introduction

0.0.1 The Dawn of Personality

In 1932 William McDougall (1932) wrote, in the first issue of what would later become the *Journal of Personality*, "Personality may to advantage be broadly analysed into five distinguishable but separable factors, namely, intellect, character, temperament, disposition, and temper...each of these is highly complex [and] comprises many variables." While Digman (1990) is quick to point out that this use of the term "factor" most likely is quite far removed from the definition commonly adopted in the modern field of personality study, it is clear that a new era of conceptualising personality in research was dawning in the 1930's. McDougall's characterisation, though lacking in substantive evidence, is echoed not long after by Louis Thurstone (1935) who performed factor analytic research on a set of 60 personality adjectives used in an observer report questionnaire and, quite interestingly, identified five personality factors. While the direct thrust of Thurstone's was not directly followed up on, lexical studies of personality continued.

The origins of codifying personality through language reaches all the way back to 1884 when Sir Francis Galton (1884), investigating the measurement of character in man and finding similarities between fathers and sons as well

as between twins and siblings, noted that often the most important individual differences in human interaction are often encapsulated in single words. Known as the "lexical hypothesis," this idea has formed the bedrock of factor analytic personality research.

In the interval between Galton's use of lexica as a starting point for the measurement of human characteristics relatively little development was made until the 1930's. Here we see McDougall and Thurstone's work but the continuation of the field rests largely on the shoulders of Gordon Allport and Henry Odbert. Though possibly inspired more by lexical studies proposed by Klages (1926) and conducted by Baumgarten (1933) of the German language and common personality terms contained therein than by the work of McDougall and Thurstone, Allport and Odbert continued with a lexical review in the context of psychology (Allport & Odbert, 1936). They made great progress in attempts to define a system of codification of personality and took steps to develop appropriate measurement tools to consistently apply this trait theory in practice (Allport, 1937).

With the groundwork laid, it is at this point we see the next stage of development of personality structure research defined by the systematic factor-analytic work of Raymond Cattell (1943, 1946, 1947, 1948). Based on the list of adjectives collected by Allport, Cattell worked to reorganise and reduce the comprehensive list into 171 descriptive terms which he used in his attempts to capture the dimensions of personality (R. B. Cattell, 1943). Much of Cattell's work involved multi-method measures of personality, comparing results from self-report questionnaires, observer-reported data, and lab-based experimental behaviour measurements to identify what he called primary personality traits (R. B. Cattell & Kline, 1977; H. E. Cattell & Mead, 2008). These primary traits

had to be consistent and visible across measurement types and a decade and a half of investigation revealed 46 surface traits, the observed behaviours indicating personality rather than the latent "source" traits (R. B. Cattell, Saunders, & Stice, 1957). After inter-correlating and factor analysing these surface traits, the culmination of Cattell's personality studies revealed a 16 trait primary structure found in both the self- and observer-report data (R. B. Cattell & Kline, 1977). While Cattell's 16-factor personality model has ultimately fallen largely out of favour in modern personality research (but see Primi, Ferreira-Rodrigues, & Carvalho, 2014), his methods and example generated further interest in the topic and was invaluable to the furtherance of the identification of personality structure.

Other contemporary researchers like Fiske (1949) and Tupes and Christal (1961) did not find the same highly complex trait structure and instead reinvented (to a certain degree) the pentagonal wheel of five factors accounting for the vast majority of personality. However their findings were overshadowed by the work of Cattell (and also that of Eysenck and his three personality factors (H. J. Eysenck & Eysenck, 1964)) and again the use of five factors was not adopted into the mainstream of personality research. This was in part due to the obscurity of Tupes and Christal's work. They were working with the United States Air Force in an attempt to predict the effectiveness of officers and their factor-analytic studies of a set of Cattell's scales and their identification of five factors was published as an Air Force technical report and flew under the radar of most psychologists at the time.

At least one researcher, however, had read this report and in 1963 Warren Norman replicated the five-factor structure as did Borgatta (1964) and Smith (1967). All of these studies continued to use Cattell's scales as the basis

for their items and yet none found sufficient evidence to support the complex structure championed by Cattell himself. While the five-factor structure was not new at this point, Norman was responsible for driving an important development in trait structure at what was still a quite early stage. Norman began investigating various organisational levels of these traits, coming to the conclusion that the structure of personality descriptors exists in three tiers below factors (Norman, 1967). At the basic level are the specific responses to specific situations, organised at the second level into habits, dispositions, etc. The third level further collapses these into broader groups of characteristics and finally at the top are the five factors representing the highest reduction and generalisation. Momentum continued in research of these lower-order traits and Smith (1967) and Wiggins, Hoffman, and Taber (1969) showed that they had a greater predictive utility than the higher-order factors, utilising the eternal wellspring of data that are university students and predicting educational achievement to a remarkable degree of accuracy.

It was at this point that research on personality traits sadly fell into what might be considered a "dark age" and few papers were published in the subsequent decade supporting the trait theory. The attack was many-pronged, trait research and personality in general was vilified by some (e.g. Ullman & Krasner, 1975; Wegner & Vallacher, 1977) and the behaviourist philosophy adopted by social psychologists at the time were showing that the situation wielded great influence over behaviour (e.g. Darley & Latané, 1968; Milgram, 1963). Later on, Funder and Ozer (1983) were able to show that much of the evidence against these views was neglected or ignored and often situational variables accounted for less than 15% of variance.

The renaissance from these proverbial dark ages began in the 1980's with

Lewis Goldberg's continuation of lexical analysis and the five factor model (1981). He was a strong supporter of this model and suggested that the personality structures of the major theories at the time could all be conceptualised in terms of five major dimensions (e.g. R. B. Cattell et al., 1957; Norman, 1963; H. J. Eysenck, 1970; Guilford, 1975). Reviews of past work in the context of personality factors illustrated the robustness of the idea and debate shifted from whether personality could be defined by internal, latent factors to whether there were five (Digman & Takemoto-Chock, 1981) or six (Hogan, 1991), the sixth being a division of Extraversion into two factors, Sociability and Inquisitive. This debate was resolved in support of five factors and a general consensus was reached by the late 1980's (Goldberg, 1981; Brand, 1984; Digman, 1988; John, 1989). Another highly important development during this period was the development by Paul Costa and Robert McCrae of the Neuroticism, Extraversion, Openness Personality Inventory (NEO-PI, Costa & McCrae, 1985). It is here, just over a century after Galton put forward his lexical hypothesis, that we reach our branch of the realisation of his idea that "The character which shapes our conduct is a definite and durable 'something,' and therefore...it is reasonable to attempt to measure it" (Galton, 1884)).

While there still exist schools of thought based on a variety of other personality structures (e.g. H. J. Eysenck & Eysenck, 1985) and debate has been heated (see Costa Jr & McCrae, 1992a, 1992b; H. J. Eysenck, 1992a, 1992b), the five factor model continues to enjoy strong support and widespread use (e.g., Costa, Weiss, Duberstein, Friedman, & Siegler, 2014; Weiss et al., 2016; Boyette et al., 2013; Judge, Rodell, Klinger, Simons, & Crawford, 2013).

0.0.2 A Brief History of Primates

The origins of the primate order stretch back to the Cretaceous period where the earliest common ancestor of all primates faced stiff competition from reptiles and dinosaurs around 85 million years ago (mya, Martin, Soligo, & Tavaré, 2007). Twenty million years later, these early euprimates suddenly found their competition to be severely disadvantaged as a result of the major extinction event at the end of the Cretaceous and began to rapidly diverge to fill the ecological gaps. It is here where the first instances of the two major branches of the primate order begin to emerge. Known as Adapiformes and Omomyiformes, they represent the early divergence of the two primate suborders, strepsirrhines and haplorrhines (Kay, Ross, & Williams, 1997). The strepsirrhines, or primates with wet noses, later evolved into what are today lemuriformes and lorisiformes and include all of the families of lemurs and lorises respectively (Perelman et al., 2011). The other group diverged into the tarsiers and the anthropoids, the latter group containing the entirety of the species we know as apes and monkeys.

Somewhere around 20 to 27 mya, a group of these early anthropoids common ancestors managed to cross the Atlantic ocean and by doing so divided the simiform infraorder into the platyrrhines and catarrhines, or New World and Old World monkeys (Perelman et al., 2011). Though the fossil evidence from this era is relatively slim (Wilkinson et al., 2010), diversification of the Old World primates in the Oligocene era around 25 to 32 mya led to the emergence of a new type of primate (N. J. Stevens et al., 2013). This new primate was the common ancestor of the hominoidea superfamily and the first ape.

Sometime in the early to mid Miocene era, between around 23 mya to 10 mya (though the exact duration of this event is not known), a dispersal corridor

of ecologically similar land existed stretching from central Africa to southeast Asia (Chaimanee et al., 2003). Through this mosaic of tropical freshwater swamps travelled the early ancestors of the family of Hylobatidae and the hominid subfamily Ponginae. Around 20 mya these lesser apes, gibbons and siamangs, diverged from their "greater" relatives and are now found only in southeast Asia. It was about this time as well, 16.5 mya in fact, that the only nonhuman great ape outside of Africa diverged from the rest of its family (Perelman et al., 2011). Now separated by vast distances from the other ape subfamilies, orangutans exist in the wild now only on the Indonesian islands of Borneo and Sumatra. Subsequently two species of orangutans emerged, *Pongo abelii* (Singleton, Ellis, & Leighton, n.d.) and *Pongo pygmaeus* (Linnaeus et al., 1758), the former residing only on the island of Sumatra while the latter and more populous species inhabits Borneo. In 2017 a third species of orangutan was described, the first new great ape species to be identified in over a hundred years. *Pongo tapanuliensis* inhabits a small area of Sumatra and consists of only approximately 800 individuals in the wild (Nater et al., 2017). These islands have a strongly seasonal boom and bust cycle of food availability and as such orangutans tend to live largely semi-solitary lifestyles, often going for long periods of time without interacting with any conspecifics except for the rearing of young (Galdikas, 1985a, 1985b, 1985c). Males also change physically when they are at their peak, developing fleshy growths on the sides of their faces to exaggerate their size. Once this period is over they become "post-prime" and often have a large reduction in their social dominance status as well as their sociability (Galdikas, 1985a).

Though sharing some overlapping ranges, gorillas were the next great ape to diverge around 8.3 mya. Currently there are two species of gorilla, western

(*Gorilla gorilla*) and eastern (*Gorilla beringei*) (Grubb et al., 2003). Inhabiting diverse forest habitats, eastern gorillas tend to live in small, fragmented groups while western gorillas occupy a more or less continuous habitat (Doran & McNeilage, 1998). These differing ecosystems have led some subspecies to specialise to more frugivorous or stricter folivorous diets depending on availability of resources (Doran & McNeilage, 1998). Though both species share a group structure that is essentialy one dominant male and multi-female (or young all-male bachelor groups), some variation does exist in this, especially in the lowland subspecies (Watts, 1996). Dominant males in these groups are known as silverbacks due to the distinctive colouration of the hair on their backs, with subordinate males being called blackbacks for equally obvious reasons (Fossey, 1974; Harcourt, Fossey, & Sabater-Pi, 1981).

Around 6.6 mya the genera of *Pan* and *Homo* diverged, separating into the common ancestors of chimpanzees and bonobos on one side and humans on the other. Chimpanzees live in a fission-fusion society where individuals form smaller groups called "parties" within a larger community (Sugiyama, 1968; Goodall, 1986). These groups are highly fluid and flexible, with individuals associating for lengths of time from a few minutes to weeks and in numbers from one to the entire community (van Lawick-Goodall, 1968; Nishida, 1968). The dominance hierarchy is loose but male dominated with coalitions of males often supporting each other in dominance interactions (Goodall, 1986; Mitani, 2009). Females also have a dominance hierarchy which is less well defined but does influence feeding behaviour and reproductive success (Pusey, Williams, & Goodall, 1997; Pusey & Schroepfer-Walker, 2013). Relationships and cooperation between individuals are not purely based on kinship and parties are not based on genetic relationships (except in the case of pre-adult offspring and

their mothers) (K. E. Langergraber, Mitani, & Vigilant, 2007; K. Langergraber, Mitani, & Vigilant, 2009; Wakefield, 2013).

The most recent divergence relevant in the ape taxonomy is that of chimpanzees and bonobos around 2.2 mya (Perelman et al., 2011). These two species inhabit a very similar geographic area and their territories are divided by the Congo River in central Africa. It was once thought that the formation of the Congo River was the driving force behind this speciation however for this to be the case the isolation of the populations would have had to have occurred 34 mya when the river actually became a geographic barrier. Instead, it is much more likely that one or more founder groups of early *Pan* ancestors crossed the river during one of the rare instances during the Pleistocene Era when the discharge of the river decreased and was subsequently cut off from the rest of the population that would later go on to become modern chimpanzees (Takemoto, Kawamoto, & Furuichi, 2015). The group whose descendants are known today as bonobos also live in similar fission-fusion societies to chimpanzees with female dispersal though their new habitat provided a much more stable environment with less seasonality and more consistent availability of food than that which they had left (Furuichi, 2011). It is thought that these factors contributed to the lower rates of fission-fusion and both inter- and intragroup competition observed in bonobos compared to chimpanzees (Furuichi, 2011). Another major difference from chimpanzees is the non-exclusive system of female-led dominance in bonobo society and the stable cooperative relationships formed by females within communities (Vervaecke, De Vries, & Van Elsacker, 2000; J. M. G. Stevens, de Groot, & Staes, 2015). Together these factors contribute to a quite different interpretation of a fission-fusion social structure in bonobo society compared to the more aggressively dominant style

exhibited by their close relatives chimpanzees.

Backtracking somewhat along the evolutionary tree, the most distantly related primates from humans are the Lemuriformes or lemurs. Diverging from the other extant strepsirrhine lorises approximately 58.6 mya and colonising the African island of Madagascar (Perelman et al., 2011), they are now only found within the borders of the island nation and are its exclusive primate inhabitants (Richard & Dewar, 1991). With over a hundred different species and subspecies (Mittermeier et al., 2008), lemurs fill a wide range of ecological niches in a variety of habitats. Despite this plethora of diversity, there are several common characteristics amongst lemurs that make them stand out from other primates as unique. One of these is the general lack of sexual size dimorphism and a tendency towards female dominance in social groups (van Schaik & Kappeler, 1993). Many species are pair bonded and those that do live in social groups tend to have roughly equal adult sex ratios and weak non-parental female bonding for female-dominant species (van Schaik & Kappeler, 1993). The most common and well researched lemur species is the ring-tailed lemur (*Lemur catta*). This species lives in matrilineal groups with a core of adult females and one or more central males, with other males in the group and male offspring disperse from the group when they reach sexual maturity (Gould, 2006).

0.0.3 Personality in Nonhuman Animals

Use of the term 'personality' has been somewhat controversial in its application to other species (S. D. Gosling, 2008). Some researchers have instead used terms such as 'temperament' (Kagan & Snidman, 2004) or 'behavioural syndrome' (Sih, Bell, Johnson, & Ziemba, 2004) to represent what is essentially

the same idea largely in order to avoid accusations of anthropomorphism by assigning the 'human' characteristics of personality to other animals. Though there are many reasons why this substitution is not ideal, Weinstein, Capitanio, and Gosling (2008) set out three reasons why using the term 'personality' is preferable to its alternatives. Firstly, it is best to be conservative with the creation of new terms unless there is good reason. Second, using this term facilitates comparative research in personality and makes easy connections to the large body of human personality research. Finally they posit that using the term 'temperament' brings in unwanted assumptions about the traits it references because in the human literature temperament is often used to describe early and inherited traits in developmental psychology (McCrae et al., 2000). Adding to this list is the fact that specific investigations into the effects of anthropomorphism on nonhuman personality research have been investigated and shown not to influence personality ratings in any meaningful way (Weiss, Inoue-Murayama, King, Adams, & Matsuzawa, 2012).

Personality in nonhuman animals has, in some form or another, been observed in a psychological context for nearly as long as it has in humans (e.g. Pavlov, 1908/1941; Köhler, 1925; Crawford, 1938), though not without its own complexities and obstacles to reaching the state it is in today. In the early days of the field and despite work by famous and influential figures such as Pavlov (1908/1941) and later Yerkes (1939), the study of personality in other species had fallen largely by the wayside in the early 20th century. In the 1980's, Joan Stevenson-Hinde and colleagues (Stevenson-Hinde & Zunz, 1978; Stevenson-Hinde, Stillwell-Barnes, & Zunz, 1980a, 1980b) developed an instrument for assessing personality in monkeys and using this explored the structure and development of personality in this species. This questionnaire had

observers rate individuals on behaviourally defined adjectives to which a principal components analysis was applied (Hope, 1968) to extract three bipolar personality dimensions, Confident-Fearful, Active-Slow, and Sociable-Solitary (Stevenson-Hinde & Zunz, 1978). Stevenson-Hinde's research sparked, in part, a resurgence in personality research using nonhuman animals (S. D. Gosling & John, 1999; S. D. Gosling, 2008). Over the last thirty years great steps have been made in standardising the criteria for personality measurement and the various methods available have been evaluated for their various advantages and disadvantages (Freeman & Gosling, 2010).

Relevant to all measures of personality, but especially in the evaluation of multiple primate species, is the idea of the interconnectedness of evolutionary and taxonomic relationships. Comparisons between species can be used to investigate the emergence of certain traits in the evolutionary tree (S. D. Gosling & Graybeal, 2007). While correlational and associative comparisons between species can be useful for any number of aspects (Silverman & Eals, 1992; Miller, Putcha-Bhagavatula, & Pedersen, 2002), often researchers neglect to account for the interrelatedness of these species and how data on traits are not necessarily independent, being potentially shared by a common ancestor and thereby violating a basic statistical assumption (Felsenstein, 1985). In this way comparisons between the structure of personality in different related species such as great apes are next to meaningless if we do not appreciate the evolutionary context in which these traits were developed, preserved, and/or lost. For example, the presence of a factor of extraversion in humans (Goldberg, 1990), chimpanzees (King & Figueredo, 1997), and orangutans (Weiss, King, & Perkins, 2006) is much more likely to be a result of this factor existing in a shared ancestor than it is the result of independent convergent evolution just as it is

more likely for the common ancestor of great apes to have evolved without a tail than for each great ape individually to have evolved this characteristic in isolation (Ricklefs & Miles, 1994). If this lack of independence in this data is accounted for however, the study of the interrelatedness of these traits using evolutionary comparisons between species has the potential to greatly expand our understanding of why these structures exist in the way that they do and can be used inform our understanding of human psychology as well (S. D. Gosling & Graybeal, 2007; King & Weiss, 2011).

0.0.4 A Guide to Comparing Apples and Orangutans

The study of personality in other species shares several key similarities with cross-cultural personality study between groups of humans (Church, 2001; S. D. Gosling, 2001). In both there is an attempt to map out the landscape of personality in multiple populations, though in humans the differences between these populations are often language, tradition, attitudes, and customs opposed to the differences between species which are often genomic, ecological, and in fundamental social organisation. Drawing from cross-cultural literature, there are two main approaches that can be taken when studying the differences between these populations. The *emic* approach focuses on assessing individuals on traits generated from within their own culture, essentially beginning anew in each group and comparing the final outcomes. While these constructs may end up being more valid and relevant to the populations or species they are measuring personality in, it makes meaningful comparisons between species much more difficult as any true cultural differences are indistinguishable from artefacts of measurement in those individually derived measures. The other method of study, the *etic* approach, involves translating or modifying measures

developed in one culture to be suitable for use in another. The major advantage of using this approach is that any differences between the populations studied should, in theory, only stem from actual cultural differences. This approach is not without its drawbacks as well and any factors that may be unique to a particular culture may be lost in the translation (Church, 2001).

These two ideas can be applied to the study of personality between species as well (S. Gosling & John, 1998) with the application of questionnaires such as the Hominoid Personality Questionnaire (HPQ) falling squarely under the *etic* category. While *emic* studies are still very useful in investigating aspects such as behavioural correlates and unique personality features in other species (Capitanio, 1999), they do not allow us to make connections to the evolution of personality nor make clear comparisons between multiple species (Weiss et al., 2006). It was not until 1997 when King and Figueredo applied the *etic* approach to study the factor structure of personality in chimpanzees that this theory became a focus of nonhuman animal personality research.

In their study, King and Figueredo had zookeepers rate chimpanzees on 43 adjectives that made up the Chimpanzee Personality Questionnaire (CPQ). 41 of these items were taken from Goldberg's (1990) personality taxonomy and two ("clumsy" and "autistic") were added to better represent specific aspects of chimpanzee personality. They identified six personality factors, Surgency, Dependability, Agreeableness, Emotionality, Openness, and Dominance (King & Figueredo, 1997). The first five of these were later renamed to better correspond with the human personality traits they resembled (King, Weiss, & Farmer, 2005) but the sixth and largest was kept as dominance. Later studies showed that these factors were replicable and generalisable across different groups (King et al., 2005; Weiss, King, & Hopkins, 2007). Though initially

neuroticism and openness did not generalise, this is actually in keeping with human cross-cultural literature (Saucier & Goldberg, 2001) where these factors do not show as strong of a pattern in other human groups. This issue was contributed to by the limited number of items in these factors in the CPQ. Updated versions of the questionnaire with the added aim of broadening the scope to other species and in a version for orangutans (Weiss et al., 2006) and general hominoids known as the Hominoid Personality Questionnaire (King, Figueredo, & Weiss, 2006; King, Weiss, & Sisco, 2008; Weiss et al., 2009) consisted of 48 and 54 items respectively. These measures also replicated when used in different human contexts as well, generalising when questionnaires were translated into Japanese (Weiss et al., 2009). Since then the HPQ has been applied to bonobos (Weiss et al., 2015), gorillas (Eckardt et al., 2015), rhesus macaques (Weiss, Adams, Widdig, & Gerald, 2011), and brown capuchins (Morton et al., 2013) among others, each revealing a unique set of personality traits for the surveyed species.

These questionnaires are not the only ones currently in use for measuring personality in nonhuman primates however. The prime example of an independent questionnaire that can be used was developed by Stevenson-Hinde and Zunz (1978). They created an independent questionnaire using the lexical method from a pool of adjectives collected from researchers recording behaviour on rhesus macaques. This questionnaire was then used, along with the HPQ, as part of the basis of a more recent chimpanzee questionnaire created by Freeman et al. (2013). We have chosen to use the HPQ as the basis of our study largely because of its comparative value. Using the same items to assess personality in multiple species gives us a much more direct comparison and helps to avoid potential confounds of species and items while also better showing differences

in the factor composition in each species.

0.0.5 Criticisms of Nonhuman Personality

As a field, personality in nonhumans faces strict criticism regarding whether or not it exists and, if so, the extent to which it is useful. (S. D. Gosling, Lilienfeld, & Marino, n.d.). To answer these critics, we should be able to show that personality in nonhumans is both reliable and valid. Strong interrater reliability has been shown in a number of species in a variety of orders by S. D. Gosling (2001) and specifically using these questionnaires in chimpanzees (King & Figueredo, 1997; Weiss et al., 2009) and other primate species (e.g. Weiss et al., 2006, 2015; Weiss, Adams, Widdig, & Gerald, 2011). These ratings generally fall within the acceptable range of human personality scores and, as they are usually conducted by multiple raters, generally have increased reliabilities of mean scores which compensate for the often smaller sample sizes (King & Weiss, 2011).

Construct validity (Cronbach & Meehl, 1955; Campbell & Fiske, 1959) applies when subjective measures are based on expected networks of correlations connected on theoretical bases. In the case of personality, we should expect ratings of items such as "playful" to correlate with measures such as frequency of play behaviours. In nonhuman personality we see these associations exhibited in several studies (Stevenson-Hinde et al., 1980a; Uher, 2011; Uher & Asendorpf, 2008). More detailed comparisons with these correlation networks involve indirect personality measures combining into related factors and being associated with broader real-world measures. We see this association between the factors identified by King and Figueredo (1997) and their correlations. As an example, the factor of extraversion in chimpanzees is positively correlated

with social approach and gymnastic activities while agreeableness is negatively correlated with agonistic behaviours (Pederson, King, & Landau, 2005).

Anthropomorphism

Anthropomorphism is the description of the behaviour or personality of an animal in terms usually used to describe human behaviour or personality (Schilhab, 2002).This can be applied to immediate states such as "angry" or to intentional states such as those implied by phrases like "thinks that" or "knows about." The attribution of these states is a normal human reaction and occurs frequently, possibly as a result of basic social cognitive processes (Andrews, 2009; Waytz, Epley, & Cacioppo, 2010). Critics warn of the contamination of personality research in nonhumans by anthropomorphic ideas causing problems for those using instruments like the HPQ (Uher, 2008b; Wynne, 2004). While these concerns are understandable, anthropomorphism can also have some benefits and is far from incompatible with scientific study. For example it has, in a critical capacity, been shown to be helpful in understanding complex animal behaviour (Burghardt, 2007). Weiss et al. (2012) examined whether personality ratings using questionnaires were products of anthropomorphic projections or other personal biases of raters. Such biases could include ideas like "All chimpanzees are friendly," which could be held by a single rater or all raters based on cultural notions (Weiss et al., 2012). They found that ratings were not a result of personal biases but instead were indicative of inherent tendencies in individual animals (in other words, personality). This reinforces the idea that these individual differences are better explained by genetic and phylogenetic affinity rather than by anthropomorphic artefacts of rater biases.

Captive vs. Wild

When using nonhuman primates as subjects for psychological study, researchers often run into the issue of the differences between captive and wild primates. As an example of some unexpected differences, handedness has been shown in wild chimpanzees to be skewed to the left when termite fishing but no preference is shown for the left or the right hand in captive populations (Hopkins, Russell, Schaeffer, Gardner, & Schapiro, 2009). In personality research, we are generally dependent on observations from captive animals due to the restrictions of observer familiarity and ease of access (Freeman & Gosling, 2010), though there are exceptions to this (e.g. Garai, Weiss, Arnaud, & Furuichi, 2016; Eckardt et al., 2015). In theory, there should be no difference in structure between the personality of wild and captive groups due to the inherent nature of personality factors and efforts by caretakers to mimic conditions in the wild wherever possible for reasons of welfare (Yamanashi & Hayashi, 2011). However, we may observe differences due to limitations associated with keeping captive apes. Apes kept in a captive environment have ready access to food, a largely static social group, limited home ranges, and often a constant exposure to observers in the form of zoo patrons (Hewson, 2003; Keeling, Rushen, Duncan, et al., 2011). As such, individuals that possess certain characteristics such as higher extraversion and lower neuroticism are better suited to life in captivity and often live longer than those overly aggressive or affected by stress (Robinson et al., 2017). These animals are also all likely to be quite interrelated due to zoo breeding programs and the difficulty of introducing new individuals into an established community (Morin & Ryder, 1991; Weiss, King, & Figueredo, 2000). The concerns we have when using these captive individuals as a stand-in for all individuals is that they may not be comparable to the free-ranging

human population. This may in fact be quite the opposite. While there is undoubtedly evolutionary influence on human personality (Nettle, 2006; Penke, Denissen, & Miller, 2007b), modern humans are far removed from their environment of evolutionary adaptation (Symons, 1990). While humans have had 40,000 more years outside of this environment - using technology such as agriculture to adapt to their environments - for their genome to change (Hawks, Wang, Cochran, Harpending, & Moyzis, 2007), both are now largely avoiding many of the traditional selective pressures such as predation and in this regard captive animals should be equally sufficient as a comparative personality standard. It may also be more valuable to use captive animals as subjects from the standpoint of application. Personality can be used to predict problems and help improve the lives of animals in captivity and having a potentially more direct and relevant measure can lead to better predictors and better implementation of welfare programmes (Robinson et al., 2017; Watters & Powell, 2012; Weiss, Adams, & King, 2011; Weiss et al., 2009; Weiss, King, & Enns, 2002; M. Gartner & Weiss, 2018).

Chapter 1

Evolutionary aspects of personality development: Evidence from nonhuman animals

1.1 Personality Development in Nonhuman Animals

At first glance, personality seems to be counterproductive to evolutionary success. An individual from a species where personalities are present will engage in predictable behaviours when exposed to similar situations, limiting its behavioural flexibility. In theory, an individual with greater behavioural flexibility should have an advantage over more inflexible individuals, being able to adapt to a wider range of potential scenarios (Wolf, van Doorn, Leimar, & Weissing, 2007). Instead, we see patterns of reduced flexibility in the form of personality structures of varying degrees in not just humans, but a huge

range of species (S. D. Gosling, 2001). It follows then that there must be processes at work for variation in personality to be as successful and widespread an adaptation as it appears to be. Personality in modern humans undergoes clear and well-documented changes over the course of the lifespan (for a review see Specht, 2017). These developmental arcs have not developed suddenly, but have come about over millions of years through natural selection. When taking into account other factors involved in the passing along of one's genes, such as reproductive strategies and life history, the evolution of personality traits and their developmental trajectories seems to be inevitable (Figueredo et al., 2005). Here we explore leading theories as to why personality has evolved and how its variation across the lifespan can be beneficial to the evolutionary fitness of an individual.

1.1.1 Life History Theory

Life history theory, first proposed by MacArthur and Wilson (1963) in their paper An Equilibrium Theory of Insular Zoogeography, is the idea that different expectations of evolutionary fitness require different systematic behavioural choices to be successful. These systematic behaviours tend to fall into two broad categories of reproductive strategies, r-strategy and K-strategy. r-strategists are named for their reliance on a high ecological growth rate for success and K-strategists are so called because their populations stay close to carrying capacity, the number of individuals their environment can sustainably support. The stereotypical r-strategist has a short lifespan, high reproductive rate, and a high mortality rate while the typical K-strategist has a long lifespan with low mortality and reproductive rates. To deal with the predicament presented by its fleeting lifespans and successfully pass on its genes to the next generation,

the r-strategist will attempt to have as many offspring as possible as early as possible in the short time available to it. This provides the r-strategist with a numerical advantage against the high mortality rate it is faced with in the hopes that a small percentage of its offspring will grow and reproduce quickly to continue the cycle. The classic example of an r-strategist is the mayfly, *Ephemeroptera spp.*, each individual laying and fertilising millions of eggs during their short lifespan (Brittain, 1990). K-strategists, on the other hand, only have a small number of offspring at much longer intervals than the r-strategists. K-strategists invest a great deal in their few offspring, for example by providing parental support until the young are able to fend for themselves. In relation to the mayfly, humans may be considered K-strategists (Kaplan, Hill, Lancaster, & Hurtado, 2000), having usually only one child at a time and caring for them many years after they are born.

Life history theory has also been applied at the level of individuals within a species (Biro & Stamps, 2008; Figueredo, Vásquez, Brumbach, & Schneider, 2007). Individuals that have high future expectations of success, and therefore a great deal to lose should injury or death befall them, should be more averse to risk-taking behaviour than an individual with lower expectations. This risk avoidance is applicable to any number of commonly occurring situations, leading different individuals to consistently respond in different ways to the same stimulus. Eventually, these consistent and predictable patterns of behaviour can be reasonably referred to as personalities. As a result of this evolutionary theory of personality, we would expect personality structures in most species to contain some factor related to risk aversion and indeed this is what research has shown. Timidity/boldness come up time and time again at a fundamental level in the personality structure of a variety of species (e.g. Carere & van

Oers, 2004; Sinn, Gosling, & Moltschaniwskyj, 2008; Sneddon, 2003). The details of personality differences has been summarised at length elsewhere (see S. D. Gosling, 2001).

At its core, life history theory represents a strategic allocation of resources to maximize reproductive success. To maximize fitness, a trade-off must take place in regards to how energy is allocated. Where survival is not guaranteed, it is more prudent to invest energy in reaching sexual maturity as quickly as possible and then pouring energy into reproduction at the expense of longevity. However, when safety is more assured, it may be better to invest in one's own longevity and the longevity of a few well cared for offspring so that many successful offspring can be produced. These variable reproductive strategies provide us with an explanation of the origins of personality and its prevalence across taxa.

1.1.2 Balancing Selection

Life History Theory, however, is only the beginning of the evolution of personality. The five human personality factors that appear to be present in most, if not all, human cultures (McCrae, Terracciano, & 78 Members of the Personality Profiles of Cultures Project, 2005), is more complex than timidity versus boldness. Variation in the levels of personality factors is thought to be maintained by one or more forms of balancing selection (D. M. Buss, 2009; Nettle, 2006). Balancing selection occurs when variation in a trait is maintained over generations because different levels of a trait are adaptive in different environments to a similar degree. Balancing selection can maintain variation in personality via any one of several mechanisms (Penke, Denissen, & Miller, 2007a).

One such mechanism is environmental heterogeneity or, putting it more

straightforwardly, differences in personality are selected differentially across geographical locations. Various environments select for different personality traits which in turn select for variation in the population. Genetic analysis has shown that people with a migratory ancestry, such as early austronesians, have a higher prevalence of some alleles related to novelty seeking or extraversion than those from sedentary populations (Chen, Burton, Greenberger, & Dmitrieva, 1999; Eisenberg, Campbell, Gray, & Sorenson, 2008; Matthews & Butler, 2011). This supports the idea that variation in personality could be selected for by the varying environmental demands of a geographical location. Balancing selection can also interact with the effects of social structure (see below) when social roles are influenced by the environment.

Another, possibly more influential type of balancing selection, is frequency-dependent selection. This form of selection occurs where the evolutionary fitness of a particular strategy or behaviour is proportional to the frequency with which it occurs in the population (Ayala & Campbell, 1974). A prime example of frequency dependent selection is in the phenomenon of 'social loafing' (Latané, Williams, & Harkins, 1979). A social loafer is one who allows others to do a majority of the work required to reach a goal. However, this strategy stops being effective if the frequency of loafers in the population becomes too high. Therefore, for loafing to be a viable strategy, the frequency of loafers in the population must be proportionate to the non-loafers.

A further possibility is that personality traits each have their own advantages and disadvantages (Weiss, 2018). Neuroticism, for example, may have some benefits from increased vigilance against danger, but ultimately has negative effects on long term health due to added stress (Nettle, 2006). The same mechanisms can apply to age and development. Behavioural plasticity with

changing population dynamics and the changing nature of interactions with conspecifics with age can alter the frequencies of trait clusters selected for (Wolf & Weissing, 2012). This provides an advantage to individuals whose personality develops in accordance with these changes who can then use their increased fitness to propagate genetic predispositions towards adaptive developmental arcs of personality factors.

While balancing selection may provide an explanation for a further evolution of variation in basic personality, it does not fully explain the extent to which this variation follows consistent developmental trajectories within the individual over time (for the case in humans see Roberts, Walton, & Viechtbauer, 2006 for a review). Complementing the application of life history strategies and frequency-dependent selection to the evolution of personality, sociability is another common characteristic of species with more complex personality trait structures that has contributed to the structure we see today (Wolf & McNamara, 2012).

1.1.3 Sociability

A key attribute of any personality trait is consistency. Personality can and does change within an individual over time but the way and rate of changes are consistent and predictable, and thus re-test correlations tend to be high (Bell, Hankison, & Laskowski, 2009; Roberts & DelVecchio, 2000). One theory as to why this is the case has to do with the social contexts that accompany species in which personality has been described. Being part of a community means interacting with conspecifics on a regular basis and some of these individuals are bound to respond differently to stimuli due to chance, personality, or any number of other plausible reasons. When these differences involve social inter-

action, individuals may respond to each other's behaviours and subsequently modify their own behaviour based on the information gained through these interactions. This phenomenon is known as social responsiveness and is advantageous because it allows individuals to tailor their responses to each other in a way that may be more beneficial in the future (Dall, Houston, & McNamara, 2004; Johnstone, 2001; Johnstone & Manica, 2011; Wolf, Van Doorn, & Weissing, 2011). For example, if an individual knows that another individual is less likely to share food if they are aggressive towards the other, in future interactions they may withhold aggression regardless of whether food is present. This change in behaviour increases the chances of cooperation and reduces the negative effects that would arise from competition, thereby benefiting the individual. However, social responsiveness is only possible if the behaviours involved are consistent over time and applicable information can be obtained from previous observations and interactions. In this way, social responsiveness is only valuable if there is consistency in behaviour (Dall et al., 2004). By the same token, the value of being consistent in one's behaviours is greatly increased when other individuals are socially responsive (Wolf et al., 2011). This interaction, coupled with frequency-dependent selection, is proposed to explain the emergence of consistent behavioural tendencies over time. It should also be noted that, alternately, social responsiveness can evolve first, giving rise to frequency-dependent selection and consequently consistent personalities.

Social responsiveness and the specialisation of sociability into specific roles can also influence personality development. With the selective pressure of reducing conflict between social partners, changes in social roles with age and changes in the personality traits most beneficial to success in these roles strongly support the development of personality over the lifespan (Bergmüller

& Taborsky, 2010). Through the lens of the theories of frequency-dependent selection and social responsiveness, it becomes clear that personality and personality development are adaptations that evolved over millions of years and continue to be adaptive for a large number of species today.

1.1.4 The Comparative Method

Up to this point most of the evidence presented for the evolution of personality has been theoretical, simulated, or based on our knowledge of animal behaviour. The question remains, how can we more directly study the evolution of human personality? The answer to this question lies in comparative research (S. D. Gosling & Graybeal, 2007; Harvey & Pagel, 1991). By studying the personality structures of related species such as chimpanzees (*Pan troglodytes*) and orangutans (*Pongo spp.*), we can, using deductive reasoning, begin to piece together a model of what our early human ancestors' personality may have been like a few million years ago (Hobolth, Christensen, Mailund, & Schierup, 2007). As we have seen in personality studies of nonhuman animals (Figueredo et al., 2005; D. M. Buss, 2009), personality is largely conserved evolutionarily and appears to be linked to genetics (Bouchard & Loehlin, 2001; Yamagata et al., 2006; Kain, Stokes, & de Bivort, 2012). However, it is very difficult at the moment to identify specific genes related to personality traits and that task is left to future researchers using fully sequenced genomes or a genome-wide association study (e.g. Bae et al., 2013). This approach can also be, and has been, used to address questions about personality development (King et al., 2008; Weiss & King, 2015). Specifically, by comparing how personality develops over the lifespan in great apes and other nonhuman primates with human personality development, we can begin to infer approximately when particu-

lar aspects of human personality evolved and what relevant selective pressures may have been influential in the process.

Factor structure in nonhuman primates The starting point for our work and that of our collaborators has been the identification of differences and similarities in the covariation (or structure) of a common set of traits. The starting point for this work was the identification of traits in Goldberg's (1990) taxonomy of the Big Five that could be applied to assess personality in chimpanzees (King & Figueredo, 1997). They found that a clear factor structure of personality existed in chimpanzees, consisting of five traits comparable to the human Big Five and a sixth trait, Dominance. Since then, these traits, as well as later versions of their questionnaire that have included other traits have been used to assess personality in several nonhuman primate species (Adams et al., 2015; Konečná et al., 2008; Konečná, Weiss, Lhota, & Wallner, 2012; Morton et al., 2013; Weiss, Adams, Widdig, & Gerald, 2011; Weiss et al., 2006), and even deer (Bergvall, Schäpers, Kjellander, & Weiss, 2011).

Other researchers, beginning at different sets of traits, have also gathered data on a variety of species. The most prominent such example would be the work started by Joan Stevenson-Hinde and her colleagues (see Stevenson-Hinde & Hinde, 2011 for a history and review). To explore the structure of rhesus macaque personality they used a set of traits sampled from Sheldon's studies of personality and somatotypes, generalised human physique categories, in humans (Sheldon, 1942). The "Madingley Questionnaire" developed by Joan Stevenson-Hinde and Marion Zunz (1978) has since enjoyed widespread use across multiple taxa (Freeman & Gosling, 2010).

We do not wish to dwell on differences in the structure of personality across

different species here. However, it is worth describing some findings to illustrate how interspecies differences allow the opportunity to understand the origins of personality domains. In chimpanzees instead of the five factors typically found in humans (McCrae & Costa, 1997b), the most plausible personality structure comprises five human-like factors and a sixth factor labelled dominance (King & Figueredo, 1997) Dominance is a broad factor indicating an individual's propensity to exhibit dominant behaviour in social interactions with conspecifics. Individuals high in dominance tend to be more assertive over others when interacting and often rise higher in the social order (King & Figueredo, 1997). Four of these factors, dominance, extraversion, conscientiousness, and agreeableness, have been clearly replicated in other samples measured on these traits (King et al., 2005; Weiss et al., 2009, 2007). Moreover, studies of different samples of chimpanzees that were assessed using other sets of traits (Dutton, 2008; Freeman et al., 2013) have identified, amongst other factors, neuroticism and openness factors similar to those originally identified by King and Figueredo (1997).

A later study of orangutans by Weiss et al. (2006) found evidence for five factors. Of these, extraversion, agreeableness, and neuroticism resembled their human and chimpanzee counterparts, dominance was similar to the chimpanzee dominance factor, and intellect stood out as combining traits related to human conscientiousness and openness to experience. Most recently, a study of personality in bonobos using this same instrument identified six factors (Weiss et al., 2015). These factors included assertiveness, which is comparable to chimpanzee and orangutan dominance, conscientiousness and openness, which resembled the same-named factors in humans and chimpanzees, a 'narrow' variant of the extraversion factor identified in humans, chimpanzees, and orangutans, and

the personality trait attentiveness, which, to date, has only been identified in brown capuchin monkeys (Morton et al., 2013).

These studies, and studies of other species that use overlapping sets of traits, allow us to infer approximately when certain personality factors emerged or disappeared. For example, personality factors labelled dominance, assertiveness, or confidence do not emerge in human studies using these traits, but consistently emerge in studies where nonhuman primate personality is measured using a variety of approaches (Freeman & Gosling, 2010). These traits share names with and are somewhat similar to their corresponding human extraversion facets (Roberts et al., 2006; John, Naumann, & Soto, 2008), but instead of elucidating as its own factor, items associated with dominance tend to be associated with high extraversion and low agreeableness (King & Figueredo, 1997). These findings suggest that factors related to dominance emerged early in primate evolution (or even before that) and that its absence as a consolidated trait in humans can be traced to events that occurred sometime after the ancestors of hominids and the *Pan* species parted some 5 to 7 million years ago (Hobolth et al., 2007). In addition to allowing researchers to better understand when personality factors emerged, comparing personality structures enables us to rule out alternative explanations for why they emerged (S. D. Gosling & Graybeal, 2007; Harvey & Pagel, 1991; Weiss, 2018). For example, extraversion is nominally related to sociability, gregariousness, activity, and so on. Evolutionary psychologists have thus posited adaptive explanations for extraversion that focus on the social aspect of extraversion (see, e.g. Nettle, 2006). The fact that extraversion has also been identified in orangutans, a fairly closely-related species, which can be described as semi-solitary at best (Galdikas, 1985a, 1985b, 1985c), should give these researchers pause.

There has been controversy over the use of ratings as well as basing these studies on items sampled from the Five-Factor Model (Uher, 2013). However, the reliabilities of animal personality ratings are comparable to or exceed those of human ratings and also behavioural measures (Freeman & Gosling, 2010; S. D. Gosling, 2001; Vazire, Gosling, Dickey, & Schapiro, 2007), there is little evidence of bias arising from anthropomorphism (Kwan, Gosling, & John, 2008; Weiss et al., 2012), and similar inferences can be made by studying personality using other sets of rated traits, such as the Madingley Questionnaire, or broadly sampled sets of behaviours (see, e.g. Neumann, Agil, Widdig, & Engelhardt, 2013).

Personality Development in Nonhuman Primates The comparative approach has recently been applied to address the rather contentious question of why do human personality traits develop in a way that suggests greater maturity, i.e., decreases in neuroticism, increases in extraversion, conscientiousness, and agreeableness, and an increase followed by decrease in openness to experience (McCrae & Costa, 2003)? Two broad theories have been put forward to explain these developmental trends. Five-Factor Theory claims that these trends have biological and genetic origins (McCrae & Costa, 2003). Evidence supporting this theory includes age-related trends, similar in both direction and magnitude, across cultures (McCrae et al., 1999, 2000, 2005), heritabilities of personality domains ranging from .4 to .6* (Bouchard & Loehlin, 2001), the presence of common genetic underpinnings of personality structure in different cultures (Yamagata et al., 2006), and the presence of common genetic effects that underlie the stability of personality factors as well as their developmental trajectories (Bleidorn, Kandler, Riemann, Angleitner, & Spinath, 2009;

McGue, Bacon, & Lykken, 1993; Viken, Rose, Kaprio, & Koskenvuo, 1994).

On the other hand, the social-investment principle states that age-related personality changes are a result of individuals investing in particular social roles that change during the course of people's lives (Helson, Kwan, John, & Jones, 2002). Examples of social roles believed to be important in this regard, include starting work, becoming married, and becoming a parent (Roberts, Wood, & Smith, 2005). Evidence has been put forward in support of the social-investment principle. For example, a meta-analysis of cross-sectional studies found that the degree to which people invested in their jobs, families, religions, and volunteerism was associated with higher conscientiousness and agreeableness, and lower neuroticism (Lodi-Smith & Roberts, 2007). Moreover, the associations just described were greater among those who were more committed to these social roles (Lodi-Smith & Roberts, 2007). Further evidence for this theory comes from a study of age differences in personality in 62 different countries (Bleidorn et al., 2013). This cross-cultural study found that neuroticism declined more steeply and conscientiousness increased more steeply in those countries where the transition to the work force started earlier, and that openness increased more slowly in countries in which the transition to family life started earlier. Finally, the social-investment principle's proponents cite the same behavioural genetic studies as its opponents do, though they highlight pervasive findings that nonshared environmental influences influence personality development (Roberts et al., 2005).

Prior to discussing these theories in light of research on nonhuman primates, it is important to note that these competing theories are not mutually exclusive, and that, to date, the studies conducted do not decisively rule one or the other out. The question therefore remains: which theory provides us with a more

complete understanding of human personality development? The comparative method, although still not providing a definitive answer, advances the argument for Five-Factor Theory over social-investment. Namely, it enables us to rule out explanations for these trajectories that rely upon present day human social and cultural constraints.

Although other studies have investigated personality development in various species of nonhuman primates like pig-tailed macaques (see, e.g., Sussman, Mates, Ha, Bentson, & Crockett, 2014) and other animals such as wild blue tits (see, e.g., Class & Brommer, 2016), we will turn to two of our studies, namely as they set out to directly compare the developmental trajectories of humans, chimpanzees, and orangutans on comparable personality dimensions. The first study investigated cross-sectional associations between age and personality in chimpanzees and compared these to cross-sectional associations between age and personality in humans (King et al., 2008). After scaling age to compensate for the fact that chimpanzees develop and mature approximately 50% more rapidly than do humans, King and his colleagues found that the magnitudes of the associations between age and the five human-like chimpanzee personality factors were similar to those found in humans. As noted in their discussion, these largely comparable age effects simply cannot be explained as being the products of social roles related to work, family, volunteerism, or religion, and the comparable magnitudes are not what one would predict given the inarguably large impact that culture has on human lives. In addition to these similarities, there were some interesting deviations from this pattern. In particular, although the trajectories were similar in direction, male and female chimpanzees differed in the size of these effects: agreeableness was associated with greater age-related increases in females as were activity (a facet of ex-

traversion) and possibly tameness (a facet of conscientiousness). As noted by the authors, these differences appeared to reflect a period of aggressive tendencies in male chimpanzees that would be consistent with the heightened inter-male aggression in this species (Wrangham, Wilson, & Muller, 2006).

These results would appear to support Five-Factor Theory, but, of course, they do not rule out an alternative explanation, namely that broader social effects common to humans and chimpanzees play a confounding role, reducing the socio-behavioural independence of the species in question. To attempt to rule out this explanation, Weiss and King (2015) compared the developmental trajectories of chimpanzee personality factors with those of orangutans, which, as we noted before, are semi-solitary as opposed to being highly social like the chimpanzees and humans. Because of the different personality structures, the comparisons were limited to four overlapping personality factors - dominance, extraversion, neuroticism, and agreeableness - of which only the latter three are shared in common with humans. Weiss and King (2015) found that the magnitudes of age effects were comparable to those of humans and chimpanzees. Moreover, like humans and chimpanzees, older orangutans were lower in extraversion and neuroticism. On the other hand, contra findings across human societies and in chimpanzees, older orangutans were less agreeableness than younger orangutans. Finally, unlike chimpanzees (but like humans), there was no evidence for a prolonged period in males marked by aggression; save agreeableness, the developmental trends for male orangutans resembled those of female orangutans, female chimpanzees, and therefore both male and female humans.

These findings suggest that the declines seen in in Extraversion and Neuroticism in both orangutans and in chimpanzees follow trajectories of devel-

opment that are phylogenetically rooted as opposed to being a result of social pressures. Again, if these development trends were socially instead of evolutionarily based, we would expect changes, and perhaps especially those related to extraversion to be reduced or even non-existent in a semi-solitary species. The parallels seen here thus rule out the possibility that these changes came about as a result of individuals' investments in their particular social roles within a highly social community (Roberts et al., 2005). They also rule out the influence of social roles related to maintaining a family as, unlike humans, males of both species do not contribute to caring for their offspring (Galdikas, 1985a, 1985b, 1985c; Goodall, 1986).

The contrast between the developmental trajectories related to agreeableness may be most straightforwardly explained as indicating that the tendency for agreeableness to increase with age reflects selection against growing disagreeableness in societies where individuals benefit from developing and maintaining cohesive bonds in adulthood. Alternatively, this could reflect the composition of the agreeableness factor, which, in orangutans, includes some traits related to extraversion (Weiss & King, 2015). The finding of similar age-related decreases in agreeableness in white-faced capuchins (Manson & Perry, 2013) contradicts the previous explanation because this species' social structure is similar to that of chimpanzees (Aureli et al., 2008). However, given that white-faced capuchins are a New World monkey species and are thus only distantly related to humans, chimpanzees, and orangutans (Steiper & Young, 2006), more data needs to be collected before we can firmly rule out the possibility that the different social structures of chimpanzees and orangutans are responsible for these differences.

As Weiss and King (2015) noted, the findings concerning chimpanzee and

orangutan personality development suggest that frequency-dependent selection may have played a role in the evolution of developmental trajectories in personality and in the cross-cultural differences observed by Bleidorn et al. (2013). Briefly, selection may disfavour those individuals whose personality trajectories differ from that found in the population. At the species level, for example, male chimpanzees who do not maintain a personality profile characterized by intense aggression into adulthood, are less likely to survive and reproduce than those who do maintain such a profile. At the level of cultures, human men and women who live in a country full of 'go-getters' will be at a disadvantage if the rate at which their conscientiousness increases is less than that of their countrymen and women. These men and women, unless they move to more 'laid back' pastures, are more likely to be out-competed and thus less likely to leave descendants.

We can see that it is likely developmental arcs in personality are deeply ingrained in our evolutionary past. However, personality development is not likely to be a product of any one evolutionary pressure or set of circumstances. It is a result of a multitude of situations, from as basic a genetic standpoint as life history theory and reproductive success to the subtleties of gradual and nuanced changes in social roles within communities.

Identifying the circumstances involved and how much they contribute to the evolution of personality development is a formidable task. However, with advances in nonhuman personality research, it is possible to start moving beyond theoretical frameworks and begin to explore this question using deductive comparisons between the phylogenies and social structures of the nonhuman animals in which personality and developmental trajectories have been identified. Creating a more complete picture of how and why personality develops

thus requires further studies of developmental trajectories in nonhuman primates, and in other species, too. Fortunately, such research is underway and we have no doubt that it will produce interesting results.

Chapter 2

A facet-level analysis of personality in chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), orangutans (*Pongo spp.*), and gorillas (*Gorilla spp.*)

2.1 Introduction

2.1.1 Five-Factor Theory of Personality

Stemming from Galton's (1884) characterisation of the lexical hypothesis over a century of research has led to the concept of a five-factor model of personality. Building on lexical work by Allport and Odbert (1936), factor analysis of personality descriptors by R. B. Cattell (1943), Norman (1967), and Goldberg

(1981), Costa and McCrae (1985) developed a questionnaire intended to measure the five basic traits of personality. These factors, as measured by Costa and McCrae's scales, the NEO-PI and later the NEO-PI-R (Costa & McCrae, 1992) have been shown to be robust and consistent across samples (McCrae & Costa, 1997b), cultures (McCrae et al., 2005), and ages (Costa & McCrae, 1982). Though there is some variation in factor score trends in some of these groups and evidence for internal change with age (Costa & McCrae, 2002), the structure itself remains constant.

These questionnaires were generated through factor analysis of a series of statements that the subject rates on a one to five scale from "strongly disagree" to "strongly agree" based on their agreement with the statement. For example, one might strongly agree with the statement "I am the life of the party" and rate that accordingly (Costa & McCrae, 1992). The data from these items are then reduced into a smaller number of factors, giving us the final factor structure. Several of these questionnaires also contain lower-order traits called facets (Costa & McCrae, 1995a). These facets allow for more detailed approach to analysis and application than the higher-order factor analytic domains. From our example above, this same person might only have an average Extraversion score despite their high ratings on some facets because it is balanced by low ratings on others. These may align with different facets within Extraversion and a highly Active person may have low Assertiveness (two of the facets within Extraversion). Looking at a factor level, we would only see the single overall score but using facets we can extract a great deal more useful information. Analyses using these lower-order facets have much greater predictive power than broad factors (Paunonen & Ashton, 2001) and are often used in applied research.

Costa and McCrae, when identifying these facets for their Five-Factor Model, decided on six facets for each factor (Costa & McCrae, 1995a). In their explanation of the rationale behind selecting six facets they posit that this number is appropriate "not because each (factor) is naturally divisible into six parts, but because at least six distinctions were suggested by the literature, and more than six scales would tax the user's ability to learn and remember the facets." They set criteria for their facets of being consistent with theory and measurement, comparable in breadth, and also as distinct as possible from one another (Costa & McCrae, 1995a). These facets have since been validated (McCrae & Costa Jr, 1992) and have provided a useful basis for comparison the study of health outcomes (Costa et al., 2014), political beliefs (Kandler, Bleidorn, & Riemann, 2012), music preferences (Rentfrow & Gosling, 2003), and more.

There is an argument however that it may be more useful to use facets that are derived statistically rather than these categories put forward by Costa and McCrae. Boyle (2008) argues that a first-stratum personality measure, like the facets of the NEO-PI-R or Cattell's 16 personality factors (R. B. Cattell, Eber, & Tatsuoka, 1970), measure a greater proportion of variance than higher stratum models like the Five-Factor Model (also see Quirk, Christiansen, Wagner, & McNulty, 2003). Debate also exists on the basic nature and general usefulness of the Five-Factor Model, touching on several of the same points of explanation of variance amongst other things (Costa Jr & McCrae, 1992a, 1992b; H. J. Eysenck, 1992a, 1992b). More recent research has taken this idea further, using the even lower stratum of individual personality items or "nuances" (made up of one or two related items) as a measure with better predictive ability and finer detail (McCrae, 2015; Mõttus, Kandler, Bleidorn,

Riemann, & McCrae, 2017; Mõttus et al., 2018, and see Chapter 3).

Criticism of Five-Factor Model, and by extension its facets, has also been called into question for potentially being not purely data-driven but constructed to fit with existing popular five-factor dimensions (for debate see Block, 1995a; Costa & McCrae, 1995b; Goldberg & Saucier, 1995; Block, 1995b). To give these criticisms a wide berth, it would be advantageous when developing a new facet scale to utilise in the first instance a more explicitly data-driven technique. This is especially true for areas such as nonhuman animal personality as there is a much shorter history of research (Weiss, King, & Murray, 2011) compared to human personality.

A point to note before continuing is the limitation of semantic meaning in the labels of domains. Factor analysis is, at its core, a variable-reduction procedure where large numbers of items are organised into a few factors summarising the intercorrelations therein (Goldberg & Digman, 1994). These factors (and their higher and lower organisational strata) are then assigned labels that correspond generally to a summary of the meaning of the items they represent. Where we can potentially run into problems and mischaracterisations in our research is when these labels are given undeserved weight and used primarily based on their semantic meaning rather than the constructs they represent. To illustrate the issue, we can look at the N4 facet of neuroticism, known as depression (Costa & McCrae, 1995a). If we were to look for correlations between personality facets and clinical disorders, we cannot assume a correlation will exist between diagnoses of major depressive disorder (American Psychiatric Association, 2013) and the facet of neuroticism simply because they share a label (Farmer et al., 2002). In the case of personality traits the whole should not be greater than the sum of its parts and we must be mindful of limiting

our assumptions.

The fact that the structure of human personality is so consistent and so universal itself raises further questions, such as how and why did this specific structure come about? In an ideal world, we would be able to go back in time to the many human ancestors over the last few million years and apply the same questionnaire to them directly, thereby creating a set of directly comparable factor structures.

One of the best options available to study early personality is to study personality in our nonhuman relatives. Personality structure in chimpanzees, our closest living relative with whom we share a common ancestor from approximately five to seven million years ago (mya, Perelman et al., 2011), consists of similarly stable and consistent factors (King & Figueredo, 1997; Weiss et al., 2007; King et al., 2005, 2008). These factors, though largely comparable, are not identical to human factors and are also joined by a sixth factor called Dominance. This then sets us on the path of backtracking through the phylogenetic tree searching for greater and greater differences that correspond to evolutionary distance. In this paper, we limit our focus to the study of personality in great apes.

2.1.2 Nonhuman Primates

All primates shared a common ancestor approximately 85 mya and underwent rapid adaptive radiation to fill niches left open during the mass extinction at the end of the Cretaceous period 65mya (Martin et al., 2007). The superfamily hominoidea, known as hominoids or more commonly apes, diverged from other primates between 32 and 25 mya (Perelman et al., 2011; N. J. Stevens et al., 2013). The lesser apes, gibbons and siamangs, further split around 20 mya and

the great apes - orangutans (16.5 mya), gorillas (8.3 mya), a common ancestor of chimpanzees and bonobos (6.6 mya), and humans (0.0 mya) emerged later (Perelman et al., 2011). Chimpanzees and Bonobos split from each other most recently, around 2.2 mya after a common ancestor crossed the Congo River during the a period of low discharge which later resurged, separating the home ranges of the species (Takemoto et al., 2015).

Comparisons between species can be used to investigate the emergence of certain traits in the evolutionary tree (S. D. Gosling & Graybeal, 2007). Although correlational and associative comparisons between species can be useful for any number of aspects (Silverman & Eals, 1992; Miller et al., 2002), often researchers neglect to account for the interrelatedness of these species and how data on trait studies are not necessarily independent, being potentially shared by a common ancestor and thereby violating a basic statistical assumption (Felsenstein, 1985). In this way comparisons between the structure of personality in different related species such as great apes are next to meaningless if we do not appreciate the evolutionary context in which these traits were developed, preserved, and/or lost. In a more optimistic view, the study of the interrelatedness of these traits using evolutionary comparisons between species has the potential to expand our understanding of why these personality structures exist in the way that they do and can inform our understanding of human psychology as well (S. D. Gosling & Graybeal, 2007; King & Weiss, 2011; Weiss, 2018).

Personality structures in these species are believed to differ as a result of selective pressures, developing from a basic shy-bold spectrum (Wilson, Clark, Coleman, & Dearstyne, 1994) to the complex factor structures and social complexities of humans and other great apes (Goldberg, 1990; King & Figueredo,

1997; Weiss et al., 2006, 2015; Eckardt et al., 2015). As mentioned above, though behavioural traits may be identifiable through inspection of preserved morphology (Lister, 2014), the evolutionary development of these stable behavioural differences are impossible to infer from the fossil record (Klein, 1995, 2000). Instead we rely on comparative changes and traits in personality traits, using modern humans as readily available research standards to compare with personality structures in farther removed evolutionary cousins (Weiss, 2017). This process allows us to roughly infer, in the same way that we can infer when our ancestors lost their tails or began walking on two legs (McHenry, 1982), what the personality structure of our ancestors may have been like. The value of these comparisons is increased with the analysis of a wider range of species as it gives us a clearer picture of what traits may have evolved when and under what circumstances (S. D. Gosling & John, 1999; de Queiroz & Wimberger, 1993).

When considering the evolutionary similarity between great apes it is important to note that there are differences in social organisation that could have selective effects on personality structure (Adams et al., 2015). Humans, as the reader may be aware, live in large, complex social groups with a great deal of interaction cohesion (Wrangham, 1987). These communities emphasise interpersonal relationships and much of personality is defined by behaviours in the relation to others (McCrae, 2004). As an example of this idea, orangutans are the most solitary of the great apes due in part to the limited availability of food in their natural habitat (Galdikas, 1985b). It is therefore feasible to assume that there may be reduced pressure to maintain personality traits primarily useful in a social context. Equally, chimpanzees have a much greater emphasis on inter-individual relationships and we would expect their personality traits

to facilitate these interactions.

Chimpanzees

Personality structure in chimpanzees was identified in much the same way as it was in humans. Taking a selection of descriptive personality adjectives, paired with one or two short sentences clarifying the conceptualisation of these adjectives in chimpanzees, from Goldberg (1990) and adding two of their own, King and Figueredo (1997) developed and tested a personality questionnaire suitable for use on chimpanzees. This new metric for nonhuman personality was called the Chimpanzee Personality Questionnaire (CPQ) and consisted of 43 items on a seven point Likert scale. Data were, and still are, collected from observer reports from zookeepers, researchers, volunteers, and caretakers. An exploratory factor analysis of these ratings revealed six factors. Five of these factors are slightly modified versions of the five factors present in human personality along with a sixth factor, the largest, which was labelled "dominance." These six factors have been confirmed in numerous samples and since 1997 eleven new items have been included to create the 54 item Hominoid Personality Questionnaire (HPQ, King et al., 2006). Both scales have been shown to have high reliability and validity which has been replicated on numerous occasions (King & Landau, 2003; King et al., 2005; Weiss et al., 2007, 2012).

Dominance in chimpanzees is the first factor to emerge in analyses and also is the largest divergence from human personality traits. This factor incorporates items that in humans are distributed amongst factors such as extraversion (eg. "dominant" and "timid") and neuroticism (eg. "cautious" and "fearful"). Chimpanzees that are high in dominance are generally assertive and decisive, are less easily intimidated, and tend to be better at making allies (Weiss et al.,

2002). These items are present in questionnaires applied to humans and indeed the behaviours and tendencies they are associated with can also be useful in human society. The main reason for the differences seen may be that these traits are not as strongly emphasised in humans society and selective factors favoured other traits like extraversion-related communication instead (McCrae, Jang, Livesley, Riemann, & Angleitner, 2001).

Since the ground had been broken by chimpanzee studies using the CPQ, factor analytic assessments of personality structure using the same or expanded questionnaires have been used to identify personality structures in a wide range of species within (eg. Adams et al., 2015; Morton, Weiss, Buchanan-Smith, & Lee, 2015) and beyond (eg. Bell & Stamps, 2004; Sinn & Moltschaniwskyj, 2005; Lee, 2011) the primate order. These investigations have revealed that different species have their own personality structure.

There are some that disagree with this factor method of measuring personality in animals (Uher, 2008b) and indeed in humans (Block, 1995a, 1995b but see Costa & McCrae, 1995b; Goldberg & Saucier, 1995). Though many of these claims have been refuted (Weiss et al., 2012), further validation of the existence of personality in nonhuman animals comes from alternative measures. For example, nonhuman primate personality has also been identified in independent studies using different methods. Notably, Joan Stevenson-Hinde and her colleagues used a different initial set of traits derived from Sheldon's (1942) studies of somatotypes and personality (Stevenson-Hinde & Zunz, 1978; Stevenson-Hinde & Hinde, 2011). What this shows us is that, apart from there being multiple ways to measure personality in nonhumans, is that the consistent, predictable behaviours defining personality exist and can be codified in nonhumans with independent measures.

Bonobos

Bonobos, though sharing a common ancestor with chimpanzees only 2 million years ago (Perelman et al., 2011), still show some differences in factor structure. Bonobos exhibit a different six factor structure, possessing extraversion, openness, conscientiousness, agreeableness, assertiveness, and attentiveness (Weiss et al., 2015). The first four resemble the eponymous chimpanzee domains. The factor titled assertiveness resembles the chimpanzee factor of dominance while attentiveness, also identified in brown capuchins (Morton et al., 2013), contains items that define high dominance and high conscientiousness in chimpanzees (King & Figueredo, 1997; Weiss et al., 2007, 2009).

It is interesting to note the differences in both dominance and "dominance" between bonobos and chimpanzees. Bonobos are largely seen to have a more egalitarian style of social dominance relationships (de Waal, 1995) while chimpanzees tend more towards the despotic (de Waal, 1984; Goodall, 1986; de Waal, 2000). Based on this, we would not expect there to be as strong a reliance on dominance as a personality trait in bonobos. Some predictions suggested there would not be a dominance trait at all (Eckardt et al., 2015). This dissonance between theory and practice is ameliorated however, when taking into account the observed strong dominance hierarchies in captive bonobo populations (J. M. G. Stevens, Vervaecke, de Vries, & van Elsacker, 2007; Vervaecke et al., 2000).

Another point to note in bonobo personality literature is that a subsequent study by Garai et al. (2016) found evidence for only five factors using the HPQ and behavioural measures in 16 wild bonobos. The authors point out that their study may not paint a full picture as the subjects consisted of a small group from a single community and because several items from the questionnaire were

removed because they exhibited lower inter-rater reliabilities. In combination these issues may have reduced the stability of the factor structure (MacCallum, Widaman, Zhang, & Hong, 1999; Velicer & Fava, 1998).

Orangutans

Five factors have been identified in orangutans (Weiss et al., 2006). Extraversion, neuroticism, and agreeableness are all similar to their human and chimpanzee corresponding factors, as is dominance to its chimpanzee counterpart. Intellect diverges most from the human and chimpanzee structures as it incorporates aspects of both conscientiousness and openness to experience as observed in human personality.

The lack of a distinct trait related to conscientiousness in orangutans is something that sets their personality structure apart from those of humans, chimpanzees, and bonobos. It is thought that this absence of a conscientiousness dimension is related to the semisolitary social structure followed by orangutans spending large portions of their lives alone (Weiss et al., 2006; Galdikas, 1985b). This may lead to a reduced emphasis on aspects of this trait. Indeed, other reviews have shown that conscientiousness may be an exception rather than the norm amongst the animal kingdom (S. D. Gosling & John, 1999). That is not to say that these aspects do not exist. All of the items associated with conscientiousness in chimpanzees and bonobos are still present, the variance they account for is just wrapped up in other factors and their impact is dispersed amongst other traits like intellect and dominance.

Gorillas

Recent investigations of personality in wild mountain gorillas have revealed only four factors (Eckardt et al., 2015). There are three broad factors of dominance, openness, and sociability as well as a small fourth factor referred to as "proto-agreeableness". This factor resembles the inverse of orangutan dominance and shares items with low agreeableness in humans and conscientiousness in chimpanzees. Gorillas who are high in proto-agreeableness are generally friendly, content, and emotionally stable. Dominance in gorillas is quite similar to chimpanzee dominance, though less so with orangutan dominance. Gorilla dominance also incorporates items associated with low extraversion, agreeableness, and low openness in chimpanzees. Gorilla openness incorporates openness from other species with parts of extraversion and neuroticism and low agreeableness and conscientiousness. Sociability covers mostly extroversion and, to a lesser extent, conscientiousness and agreeableness while also correlating negatively with several species' versions of dominance.

A separate personality structure has been identified in captive western lowland gorillas. Yvonne Baur (unpublished data) collected personality data on captive gorillas and analysis of this has revealed a six-factor structure. The first factor, sociability, is similar to agreeableness in orangutans and bonobos and also to chimpanzee and human extraversion but without the "physical" aspects of these factors such as Active or Lazy. Dominance in captive gorillas is similar to bonobo conscientiousness and dominance in chimpanzees and orangutans but also incorporates some of the negative aspects of conscientiousness in the latter species. Emotionality is similar to some parts of neuroticism and negative aspects of dominance in chimpanzees and orangutans but is calibrated in the opposite direction. It also shares several items with the negative

aspects of bonobo assertiveness. Negative affect has similarities to chimpanzee and orangutan neuroticism while also containing some of the negative items associated with extraversion, agreeableness, assertiveness, and conscientiousness in the other apes. Openness is a large factor in gorillas and adds the physical aspects of chimpanzee extraversion to the items associated with openness in bonobos and chimpanzees. It also resembles the extraversion domain seen in orangutans. Conscientiousness as defined in gorillas is quite similar to the eponymous factor in chimpanzees or to intellect in orangutans or attentiveness in bonobos but with the addition of a few items associated with agreeableness and from the positive aspects of dominance.

With the limited sample sizes in both of the wild gorilla and bonobo samples, there is a risk of some sampling bias being involved in the trait structure and so the larger captive samples will be used herein.

2.1.3 Analysis

When defining their facet scales for the NEO-PI, Costa and McCrae (1995a) highlighted several guidelines and criteria for the construction of useful and meaningful facets. These guidelines are drawn from their experience creating the Five-Factor Model and many apply generally as "good practice" for factor analyses. After pointing out that the number of possible combinations of items in personality domains is practically limitless, they put forward four suggestions for good facets. Firstly, and somewhat self-evidently, facets should not be arbitrary groupings but should represent elements that closely covary within the factor. They then suggest that facets should be comparable in scope and breadth, with similar levels of distinction and specificity in each so as to facilitate direct comparison between them. Thirdly, they suggest that

it would be best if the facets were comprehensive and exhausted the domain they are representing. This, they admit, may be a two-edged sword as there are sometimes potentially problematic external correlations that, if included, could interfere with further correlational studies. The example they give is the hypochondriasis facet from Eyesenck and Wilson's (H. Eysenck, Wilson, & Jackson, 1991) representation of neuroticism that was excluded from the NEO-PI-R due to possible compromise of the scale's ability to predict health complaints and outcomes due to a lack of independence amongst measures. The last guideline put forward by Costa and McCrae is that consistency with existing constructs should be maintained wherever possible. In our research we attempted to adhere to these guidelines as much as possible.

Previous work has, however, largely limited itself in scope to these factor level analyses. Here we seek to expand upon this by identifying the facet-level structure of personality in great apes. King et al. (2008) separated the CPQ items of Extraversion into two facets, Activity and Gregariousness, defined *a priori* along the lines of physical activity and social behaviour (King et al., 2008; King & Weiss, 2011). These coincided with two facets of the same names in humans (Costa & McCrae, 1995a) and were later applied to orangutans as well (Weiss & King, 2015). Chimpanzee Conscientiousness was also bisected into the facets Predictability and Tameness. The rationale behind the creation and composition of these facets is theoretical, basing them off of conceptual similarity and the facet divisions in human domains.

In order to identify meaningful facets for nonhuman personality structures, we have decided to approach the issue from a slightly different perspective. Whereas Costa and McCrae (1995a) settled on a convenient, uniform six facets for each factor, we used a hierarchical factor analytic technique to

identify facets. This method, put forward by Goldberg (2006), involves a "top down" approach to determining factor structure. Beginning with the first unrotated principle factor, Goldberg describes imposing the number of factors on a dataset in an increasing fashion. This process then is continued until a factor appears that has no main loadings on it from any of the items. The previous number of factors is then considered the most appropriate. For example, if six factors are imposed and the sixth factor is not associated with the highest loadings of any item, then we can determine that five factors is the maximum and most appropriate structure.

There are two advantages to using this method in these cases. Firstly, due to the relative lack of literature and volume of previous research on nonhuman personality when compared to human personality research, we cannot rely as heavily on previous conventions and concepts identified in literature. This has necessitated the use of a certain amount of creativity in methods and a greater reliance on statistical methods in the development of our scale.

Another concern we have about the application of facet ideas to the HPQ is that there are far fewer items in total in the HPQ and CPQ (54 and 43 respectively) than there are in the NEO-PI-R (240). While both comprehensively cover traits at a factor level (King & Figueredo, 1997; Weiss et al., 2012), the smaller number of items in the shorter scales (eg. two items loading on Openness in the CPQ) mean that it would be impossible to have six, equally weighted and valid facets in each factor. We can see evidence of this in Saucier's (1994, 1998) comparison of the NEO-PI-R and the 60 item short form NEO-FFI. Here, defined NEO-PI-R facets are represented only moderately by the NEO-FFI and the item clusters seen in this scale correlate inconsistently with the facets they are meant to represent. That there are clear facets in

the NEO-FFI shows that brief measures can contain facets that are broader in scope and may contain fewer items.

In this study, we hope to achieve a better understanding of the lower-order personality structure of the great apes which, with the exception of a few facets defined from human data in chimpanzees and orangutans (Weiss & King, 2015), has been largely ignored. The advantages this knowledge can provide are many-fold, allowing for a more differentiated, detailed perspective that facilitates greater precision of measurement of more specific traits (Paunonen, Jackson, Trzebinski, & Forsterling, 1992; Briggs, 1989; A. H. Buss, 1989; Mershon & Gorsuch, 1988). The opportunity we have here to measure these specifics is largely a practical one. We have collected large datasets from each of the four nonhuman great apes and these together allow us to both assess the facet levels with the standards of its initial measurement in humans (Costa & McCrae, 1995a) and to compare them cross species. This study is also the first large-scale comparison of personality domains using the HPQ and related scales that compares all four species, allowing for unique insights in to the state of personality in apes and to the evolutionary pathway of these lower-order traits. Though the argument of personality domains in nonhuman apes simply being artefacts of measurement unearthed from the human personality items the original questionnaire was made from has not been supported by data (King & Figueredo, 1997; Pederson et al., 2005; Weiss et al., 2000, 2009), we have decided to keep a wide berth from these criticisms by using an entirely separate method from Costa and McCrae (1995a). While their method has certainly proved useful in humans (e.g. Samuel & Widiger, 2008; Bipp, Steinmayr, & Spinath, 2008), we wanted to begin our investigation with a less theory-driven approach to see whether these same facets would emerge or whether there are

different lower-level organisations of traits in other great apes.

2.2 Methods

2.2.1 Subjects

Chimpanzees

Subjects consisted of 533 captive chimpanzees (324 female, mean age = 16.52 years) of which 156 had full HPQ ratings while the remaining 378 had only the CPQ items. These samples were first described elsewhere (King & Figueredo, 1997; King et al., 2008; Weiss et al., 2007, 2009, 2012).

The first group consists of 100 chimpanzees (59 female, mean age = 18.4 years) from King & Figueredo's (1997) original investigation of chimpanzee personality. These chimpanzees were housed at 12 zoos in the United States participating in the ChimpanZoo program run by the Jane Goodall Institute. Added to this original sample were an additional 102 chimpanzees from other zoos participating in the ChimpanZoo program including five in the United States and one in Australia (King et al., 2008). This new sample, including the original 100, consisted of 78 male and 124 female chimpanzees with an average age of 16.5 years.

Another sample was collected from the Yerkes National Primate Research Center in the United States by Weiss et al. (2007). Data were collected on 175 new captive chimpanzees (107 female, mean age = 20.5).

For the subset of the data for which the full HPQ was available, 146 chimpanzees (86 female, mean age = 22.0 years) from seven zoos and two research institutes in Japan were rated (Weiss et al., 2009). Later, an additional four

males and six females were added from two more Japanese zoos (Weiss et al., 2012) to complete the dataset used in the present study.

Bonobos

The bonobo subjects were described by Weiss et al. (2015) and consist of captive individuals from the United States and Europe. Data was collected from five zoos in Germany, one each in Belgium, the Netherlands, and the United Kingdom as well as seven zoos and one research institute in the United States. When taken together this sample represents approximately 80% of the total population of captive bonobos on these continents. In total there were 154 bonobos (83 female, mean age = 16.2 years) included in the sample and this data was used to identify the structure of personality in bonobos.

Orangutans

The orangutan subjects used in this study were 174 (104 female, mean age = 21.7 years) captive individuals from groups described in two previous studies (Weiss et al., 2006, 2012). Orangutans were housed in 38 zoos in the United States, two in Canada, one in Australia, and one in Singapore. The original set of data from 152 orangutans was used to identify orangutan personality factors.

Gorillas

Data were collected on 203 captive individuals (115 female, mean age = 20.3) housed in 30 facilities in the United States, the Netherlands, Canada, and Japan. These data were used to determine the factor structure of lowland gorillas and only contains captive individuals.

2.2.2 Questionnaires

Personality was measured using three scales, the Chimpanzee Personality Questionnaire (CPQ, King & Figueredo, 1997), the Orangutan Personality Questionnaire (OPQ, Weiss et al., 2006), and the Hominoid Personality Questionnaire (HPQ, King et al., 2006). The reason for the use of three questionnaires is simply that the majority of the data was collected before the development of the HPQ and so to make full use of the largest amount of data available we utilise both scales.

The CPQ consists of 43 personality related descriptive adjectives that are incorporated into complete statements. These statements consist of one to three sentences and are used to put the descriptor adjectives in the context of primate behaviour. This questionnaire was developed by King and Figueredo (1997) and consists of 41 adjectives derived from the human Big Five (Goldberg, 1990) and two (Clumsy and Autistic) that were added specifically for rating chimpanzees. The HPQ adds to this set five items representing openness and neuroticism (Weiss et al., 2006) and six representing openness and conscientiousness (Weiss et al., 2009). In both measures items are given a rating on a scale from one ("displays total absence or negligible amounts of the trait") to seven ("displays extremely large amounts of the trait"). Inter-rater reliabilities (e.g. Weiss et al., 2009), internal consistencies (King et al., 2005), and test-retest reliabilities (Weiss, Adams, Widdig, & Gerald, 2011) are consistently high in studies using these measures and values are comparable to similar measures observed in human personality research (see King & Weiss, 2011).

For the orangutan personality data, 48 items were used in total (Weiss et al., 2006). The OPO consists of the 43 items of the CPQ with the addition of

five items to better represent the factors of neuroticism and openness (King et al., 2005; King & Weiss, 2011). These five items were then later incorporated into the HPQ (Weiss et al., 2009).

The questionnaires were originally developed in English, though raters from non-English speaking countries used versions translated to their native language so as to allow them to more accurately represent their interpretations (King et al., 2005; Weiss et al., 2009).

2.2.3 Raters and Ratings

Ratings of all individuals were conducted by caretakers, researchers, and volunteers, all of whom were familiar with the individual animals, with a mean length of time of between five and six years in each sample. Ideally, this familiarity would be at least one year in duration for every rater, however practical limitations and the added value of an increase in the number of ratings meant that this was not always possible. The same principle applied to the number of ratings given for each animal, ideally being more than one but in practice ranging between one and eight for each dataset.

Raters were asked to base their ratings on their overall impressions of the individuals rather than of specific instances or estimated frequencies of specific behaviours to better give a comprehensive rating of the individual animal.

2.2.4 Analyses

Hierarchical Factor Analysis

The hierarchical structure of personality facets in this study used Lewis Goldberg (2006) "Bass-Ackwards" method. Here, a secondary pair of factors are ex-

tracted from a principal one and orthogonally rotated to produce an intermediate level of analysis. This extractive process is continued by imposing increasing numbers of factors on the contents of the principal component until a factor is created on which no item has its highest loading. The preceding level is then used as the highest possible number of extracted factors. For example, if at the fourth level of imposed factors we see a factor appear on which none of the items have their highest loading, we can then determine that the lowest level of the hierarchy contains three factors. After the lowest level has been identified, we can intercorrelate the total set of factor loadings between levels to derive path coefficients and construct our hierarchical representation of the overall structure.

This was confirmed by the bassAckward function described by Revelle in the R package psych (Revelle, 2018). Here, successive factors are calculated and then factor correlations are determined following the procedures described by Gorsuch (1983).

In our analysis, we used each personality domain as a principal factor and the lowest valid hierarchical level became the facets structure for that factor. Path coefficients were then used to illustrate the connections between the factor and facet levels in detail.

Table 2.1: CPQ Extraversion

Item	Facet	Loading
Active	E1	.89
Lazy(-)	E1	.89
Playful	E1	.71
Affectionate	E2	.89
Friendly	E2	.82
Sociable	E2	.67
Solitary(-)	E3	.95
Depressed(-)	E4	.77
Imitative(-)	E5	.75

2.3 Results

2.3.1 Chimpanzees

CPQ

Extraversion Extraversion produced five facets when analysed (Fig. 2.1). Two of these were multi-item facets while the remaining three consisted of single items. The items Active, Playful, and negative aspects of Lazy grouped together in the first facet (E1). The second facet contained Affectionate, Friendly, and Sociable (E2) while Solitary, Depressed, and Imitative all were represented by their own facets.

Conscientiousness This factor was divided into three multi-item facets and three single-item facets. Negative aspects of Irritable and Aggressive made up the first facet (C2) while Predictable and low Impulsive made the second multi-item (C5) and Erratic and Disorganised made up the last (C6). Defensive, Jealous, and Reckless all had their own facets.

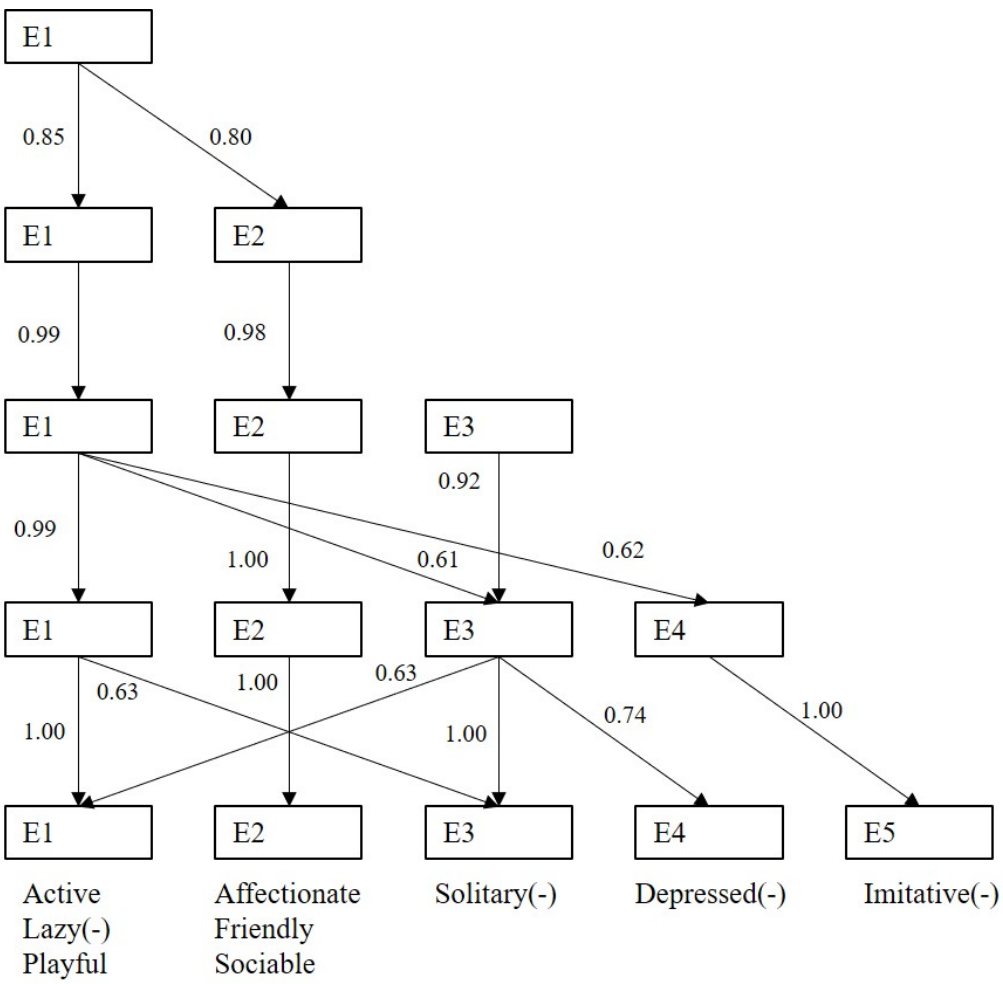

Figure 2.1: Oblimin-rotated factor diagram of items contained within the extraversion factor in chimpanzees as measured by the CPQ. This diagram shows the development of the factor structure over successive iterations of increasing factor size. Associated items are listed under their respective facet. Loadings of less than 0.60 were excluded for clarity.

Table 2.2: CPQ Conscientiousness

Item	Facet	Loading
Defensive(-)	C1	1.00
Irritable (-)	C2	.99
Aggressive (-)	C2	.34
Jealous(-)	C3	.37
Reckless(-)	C4	.87
Impulsive(-)	C5	.81
Predictable	C5	.39
Erratic(-)	C6	.69
Disorganised	C6	.59

Table 2.3: CPQ Dominance

Item	Facet	Loading
Dominant	D1	.84
Decisive	D2	.77
Bullying	D3	.81
Timid(-)	D4	.40
Cautious(-)	D4	.64
Persistent	D5	.52
Stingy	D6	.72
Independent	D7	.68
Fearful(-)	D7	.34
Submissive(-)	D8	.58
Dependent(-)	D8	.44
Intelligent	D9	.74

Dominance Analysis of dominance revealed nine facets representing twelve items. Cautious and Timid made up facet D4 while the other two multi-item facets were Independent and low Fearful (D7) and Submissive and Dependent (D8). Dominant, Decisive, Bullying, Persistent, Stingy, and Intelligent were all single-item facets.

Neuroticism Only three items are associated with neuroticism in the CPQ, Excitable, Unemotional, and Stable, were all represented by a singular facet.

Table 2.4: CPQ Neuroticism

Item	Facet	Loading
Excitable	N1	.78
Stable(-)	N1	.71
Unemotional(-)	N1	-.47

Table 2.5: CPQ Agreeableness

Item	Facet	Loading
Protective	A1	.82
Helpful	A1	.73
Sympathetic	A1	.71
Sensitive	A1	.58
Gentle	A2	.98

Agreeableness Two facets emerged from agreeableness. Protective, Helpful, Sympathetic, and Sensitive were all part of the first facet (A1) while Gentle made up its own single-item facet.

Openness Openness only consists of two items, Inquisitive and Inventive, however these did not separate and only one facet could be extracted from this factor.

HPQ

Extraversion The addition of the item Individualistic changed the facet structure slightly in the HPQ from the CPQ but five facets were still identified. Affectionate, Sociable, and Friendly ($E_{Ch}3$) and Playful, Active, and low Lazy

Table 2.6: CPQ Openness

Item	Facet	Loading
Inquisitive	O1	.87
Inventive	O1	.87

Table 2.7: HPQ Extraversion

Item	Facet	Loading
Imitative	$E_{Ch}1$	.78
Individualistic(-)	$E_{Ch}2$	.60
Affectionate	$E_{Ch}3$	.84
Sociable	$E_{Ch}3$	.66
Friendly	$E_{Ch}3$	.64
Solitary(-)	$E_{Ch}4$	.80
Depressed(-)	$E_{Ch}4$	.65
Lazy(-)	$E_{Ch}5$	.97
Playful	$E_{Ch}5$	-.50
Active	$E_{Ch}5$	-.48

($E_{Ch}5$) remained consistent but Solitary and Depressed combined into one facet ($E_{Ch}4$). Individualistic and Imitative were single-item facets.

Conscientiousness Conscientiousness consisted of nine facets, two of which contained multiple items. Facet $C_{Ch}1$ included Aggressive, Defensive, Jealous, and Irritable while facet $C_{Ch}4$ contained Clumsy and Unperceptive. Thoughtless, Distractable, Predictable, Disorganised, Quitting, Impulsive, and Erratic all were part of single-item facets. Notably here Reckless was not represented by any facet and the facet $C_{Ch}5$ which contained Predictable only had a relatively small (-0.36) negative association with its one item.

Dominance In dominance, as represented in the HPQ, fourteen factors were identified covering the fifteen items. Each facet represented one item with only Manipulative not being represented by any facet.

Neuroticism This factor was divided into two facets, each containing two of the four total items. Stable and Cool were associated with facet $N_{Ch}1$ while Autistic and Excitable were associated with facet $N_{Ch}2$.

Table 2.8: HPQ Conscientiousness

Item	Facet	Loading
Aggressive (-)	$C_{Ch}1$	.88
Defensive(-)	$C_{Ch}1$	.87
Jealous(-)	$C_{Ch}1$	.57
Irritable (-)	$C_{Ch}1$	.57
Thoughtless	$C_{Ch}2$	1.00
Distractible	$C_{Ch}3$	.96
Clumsy(-)	$C_{Ch}4$	.77
Unperceptive(-)	$C_{Ch}4$	.46
Predictable	$C_{Ch}5$	-.36
Disorganised(-)	$C_{Ch}6$	.92
Quitting(-)	$C_{Ch}7$	.94
Impulsive(-)	$C_{Ch}8$	.97
Erratic(-)	$C_{Ch}9$	.59
Reckless(-)	*N/A*	*N/A*

Table 2.9: HPQ Dominance

Item	Facet	Loading
Submissive(-)	$D_{Ch}1$	.91
Timid(-)	$D_{Ch}2$	.81
Vulnerable	$D_{Ch}3$	.78
Bullying	$D_{Ch}4$	.95
Intelligent	$D_{Ch}5$	.92
Dominant	$D_{Ch}6$	1.00
Independent	$D_{Ch}7$	.80
Persistent	$D_{Ch}8$	.85
Anxious(-)	$D_{Ch}9$	.56
Stingy	$D_{Ch}10$	.44
Cautious(-)	$D_{Ch}11$	.64
Dependent	$D_{Ch}12$	.62
Fearful	$D_{Ch}13$	.59
Decisive	$D_{Ch}14$	.64
Manipulative	*N/A*	*N/A*

Table 2.10: HPQ Neuroticism

Item	Facet	Loading
Stable(-)	$N_{Ch}1$	.92
Cool(-)	$N_{Ch}1$	.75
Autistic	$N_{Ch}2$	.56
Excitable	$N_{Ch}2$	.48

Table 2.11: HPQ Agreeableness

Item	Facet	Loading
Helpful	$A_{Ch}1$	.89
Sympathetic	$A_{Ch}2$	.45
Gentle	$A_{Ch}3$	.87
Conventional	$A_{Ch}3$	.40
Protective	$A_{Ch}4$	.76
Sensitive	$A_{Ch}4$	.52

Agreeableness The six items of agreeableness were split between four facets, two multi-item and two single item (Fig. 2.2). Gentle and Conventional were paired together ($A_{Ch}3$) as were Protective and Sensitive ($A_{Ch}4$) while Helpful and Sympathetic were each represented by their own facets.

Openness Though now containing four items (Inventive, Inquisitive, Innovative, and Curious), Openness still contained only a single facet representing all items as it did in the CPQ measure.

Table 2.12: HPQ Openness

Item	Facet	Loading
Inventive	$O_{Ch}1$	.93
Inquisitive	$O_{Ch}1$	.90
Innovative	$O_{Ch}1$	.86
Curious	$O_{Ch}1$	.75

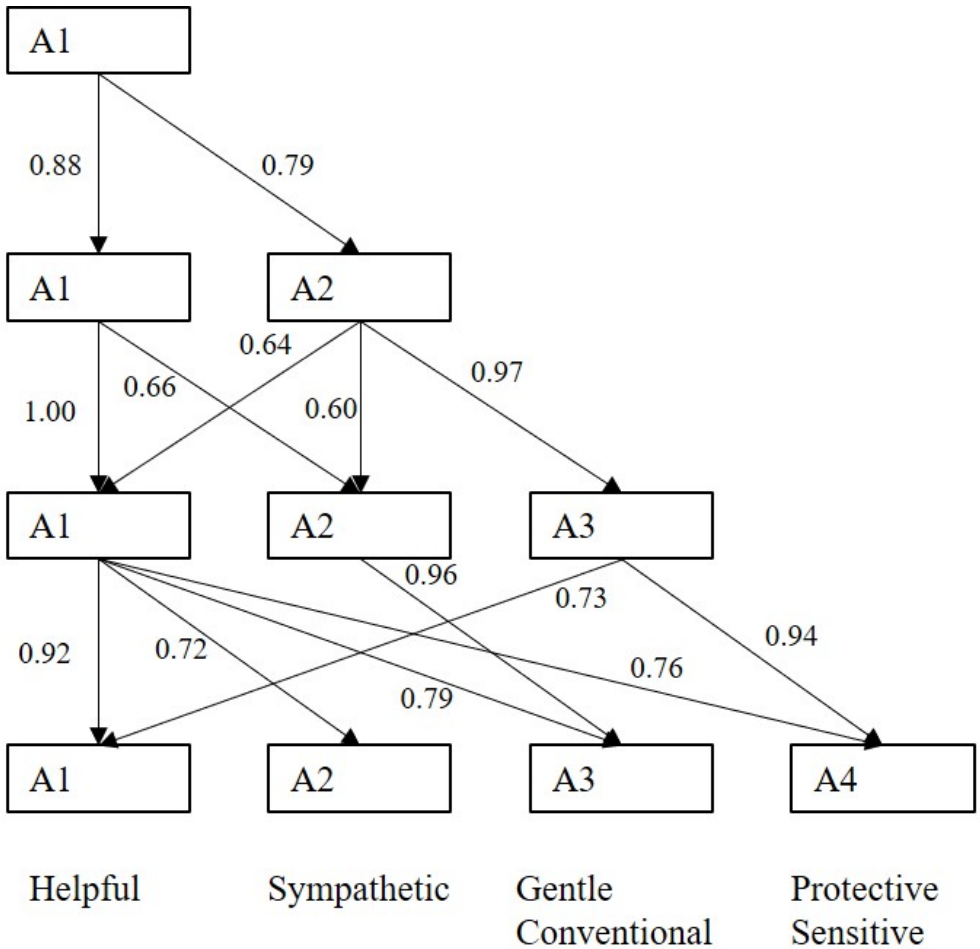

Figure 2.2: Oblimin-rotated factor diagram of items contained within the agreeableness factor in chimpanzees as measured by the HPQ. This diagram shows the development of the factor structure over successive iterations of increasing factor size. Associated items are listed under their respective facet. Loadings of less than 0.60 were excluded for clarity.

Table 2.13: Bonobo Extraversion

Item	Facet	Loading
Solitary(-)	$E_{Bo}1$	.78
Depressed(-)	$E_{Bo}1$	.60
Autistic(-)	$E_{Bo}2$	.89
Individualistic(-)	*N/A*	*N/A*

Table 2.14: Bonobo Conscientiousness

Item	Facet	Loading
Irritable(-)	$C_{Bo}1$	.73
Erratic(-)	$C_{Bo}1$	.72
Stingy(-)	$C_{Bo}2$	.63
Manipulative	$C_{Bo}2$	.56
Jealous(-)	$C_{Bo}3$	1.00
Aggressive(-)	$C_{Bo}4$	.88
Bullying(-)	$C_{Bo}4$	.51
Defensive(-)	$C_{Bo}5$	1.00
Gentle	$C_{Bo}6$	.97
Impulsive(-)	$C_{Bo}7$	.44
Reckless(-)	$C_{Bo}8$	.94
Predictable	*N/A*	*N/A*

2.3.2 Bonobos

Extraversion The bonobo factor of extraversion is made up of two facets. Facet $E_{Bo}1$ is made up of Solitary and Depressed while the second facet contains only Autistic. The item Individualistic is not represented by any facet.

Conscientiousness Conscientiousness in bonobos divides eleven items between eight facets. Three facets contain multiple items, $C_{Bo}1$ (Irritable and Erratic), $C_{Bo}2$ (Stingy, Manipulative), and $C_{Bo}4$ (Aggressive, Bullying). The remaining facets represent individually the items Jealous, Defensive, Gentle, Impulsive, and Reckless. One item, Predictable, was not represented by any facet.

Table 2.15: Bonobo Attentiveness

Item	Facet	Loading
Thoughtless(-)	$At_{Bo}1$	.82
Distractible(-)	$At_{Bo}1$	.53
Unperceptive(-)	$At_{Bo}2$	.72
Clumsy(-)	$At_{Bo}3$	.85
Disorganised(-)	$At_{Bo}3$	.56
Intelligent (-)	$At_{Bo}4$	.41

Table 2.16: Bonobo Agreeableness

Item	Facet	Loading
Friendly	$Ag_{Bo}1$	.82
Affectionate	$Ag_{Bo}1$	.64
Helpful	$Ag_{Bo}1$	.41
Sympathetic	$Ag_{Bo}1$	.38
Sociable	$Ag_{Bo}2$	.68
Protective	$Ag_{Bo}3$	.88
Sensitive	$Ag_{Bo}4$	.97

Attentiveness Attentiveness comprises of two multi-item facets and two single item facets (Fig. 2.3). The two multi-item facets represent Thoughtless and Distractable ($At_{Bo}1$) and Clumsy and Disorganised ($At_{Bo}3$) respectively while the remaining two individually contain Unperceptive and Intelligent.

Agreeableness Agreeableness in bonobos also has four facets. $Ag_{Bo}1$ contains the items Friendly, Affectionate, Helpful, and Sympathetic while the other three factors are single-item and represent Sociable, Protective, and Sensitive respectively.

Openness This factor is made up of six facets, half of which contain multiple items. Imitative and Active are grouped into one facet ($O_{Bo}2$) as are Innovative and Inventive ($O_{Bo}3$) and Playful and the negative aspects of Conventional

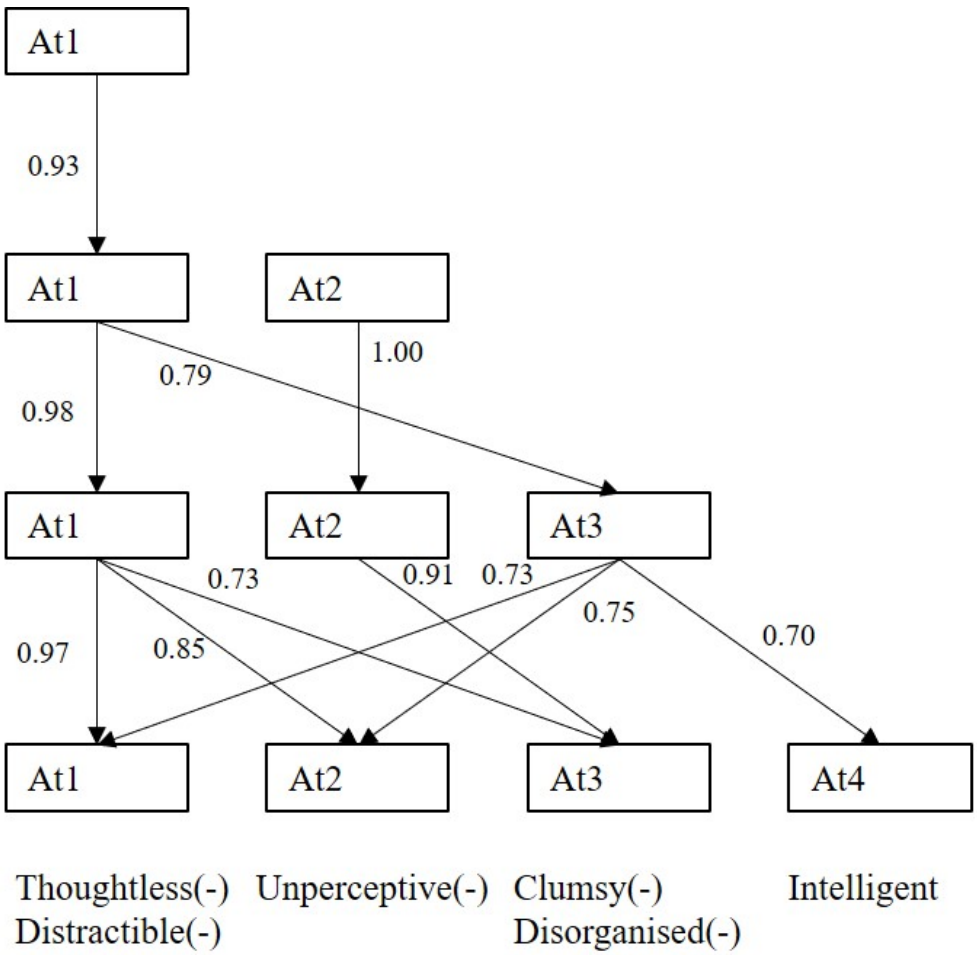

Figure 2.3: Oblimin-rotated factor diagram of items contained within the attentiveness factor in bonobos as measured by the HPQ. This diagram shows the development of the factor structure over successive iterations of increasing factor size. Associated items are listed under their respective facet. Loadings of less than 0.60 were excluded for clarity.

Table 2.17: Bonobo Openness

Item	Facet	Loading
Lazy(-)	$O_{Bo}1$	.59
Imitative	$O_{Bo}2$	.78
Active	$O_{Bo}2$	.49
Innovative	$O_{Bo}3$	.89
Inventive	$O_{Bo}3$	.75
Inquisitive	$O_{Bo}4$	.79
Curious	$O_{Bo}5$	.47
Playful	$O_{Bo}6$	.70
Conventional(-)	$O_{Bo}6$	.44

($O_{Bo}6$). Lazy, Inquisitive, and Curious are all included in single-item facets.

Assertiveness The bonobo factor Assertiveness can be broken down into six facets also. The facets of $As_{Bo}3$ (Stable, Cool, low Excitable, and Decisive) and $As_{Bo}4$ (Fearful, Timid, Anxious, and Vulnerable) are the two large multi-item facets in the set. $As_{Bo}5$ also contains multiple items, consisting of low Dependent and Independence. The remaining items, Dominant, Submissive, and Persistent, are all contained in single-item facets.

2.3.3 Orangutans

Extraversion Extraversion as defined in orangutans is made up of six facets, four of which contain multiple items. The first, $E_{Or}1$, consists of Active, low Lazy, and Imitative. Next, Playful and negative Unemotional make up $E_{Or}2$. $E_{Or}3$ contains Inquisitive and Curious while the fourth multi-item facet consists of low Conventional and Inventive ($E_{Or}4$). The remaining pair of facets are single-item and represent Depressed and Solitary.

Table 2.18: Bonobo Assertiveness

Item	Facet	Loading
Dominant	$As_{Bo}1$	.94
Submissive(-)	$As_{Bo}2$	.43
Stable	$As_{Bo}3$	.81
Cool	$As_{Bo}3$	.66
Excitable(-)	$As_{Bo}3$	.44
Decisive	$As_{Bo}3$	.41
Fearful(-)	$As_{Bo}4$	.77
Timid(-)	$As_{Bo}4$	.75
Anxious(-)	$As_{Bo}4$	.63
Vulnerable(-)	$As_{Bo}4$	.41
Dependent(-)	$As_{Bo}5$	1.00
Independent	$As_{Bo}5$	.40
Persistent	$As_{Bo}6$	.77

Table 2.19: Orangutan Extraversion

Item	Facet	Loading
Active	$E_{Or}1$	.92
Lazy(-)	$E_{Or}1$	.67
Imitative	$E_{Or}1$	.41
Playful	$E_{Or}2$	.73
Unemotional(-)	$E_{Or}2$	.49
Inquisitive	$E_{Or}3$	.92
Curious	$E_{Or}3$	.81
Conventional(-)	$E_{Or}4$	.69
Inventive	$E_{Or}4$	.43
Depressed(-)	$E_{Or}5$	.92
Solitary (-)	$E_{Or}6$	.54

Table 2.20: Orangutan Dominance

Item	Facet	Loading
Dominant	$D_{Or}1$	.90
Submissive(-)	$D_{Or}1$	.84
Persistent	$D_{Or}1$	.38
Aggressive	$D_{Or}2$	.84
Gentle(-)	$D_{Or}2$	.71
Bullying	$D_{Or}2$	.59
Stingy	$D_{Or}3$	.98
Jealous	$D_{Or}3$	.44
Manipulative	$D_{Or}4$	1.00
Defensive	$D_{Or}5$	.70
Reckless	$D_{Or}5$	.63
Irritable	$D_{Or}6$	.42

Dominance Orangutan dominance also contains six facets (Fig. 2.4). The first facet ($D_{Or}1$) includes Dominant, low Submissive, and Persistent. The next, $D_{Or}2$, is made up of Aggressive, Bullying, and the negative aspects of Gentle. $D_{Or}3$ contains Stingy and Jealous while the last multi-item facet ($D_{Or}5$) includes Defensive and Reckless. Manipulative and Irritable are represented by their own individual facets.

Neuroticism This factor has three facets. $N_{Or}1$ contains Impulsive, Excitable, Erratic, and low Predictable. $N_{Or}2$ includes Timid, Fearful, Anxious as well the negative aspects of both Stable and Cool. The third and final facet is made up of the sole item Cautious.

Agreeableness Agreeableness has only two facets in orangutans, the first containing Friendly, Sociable, and Affectionate and the other Sympathetic, Protective, Helpful, and Sensitive.

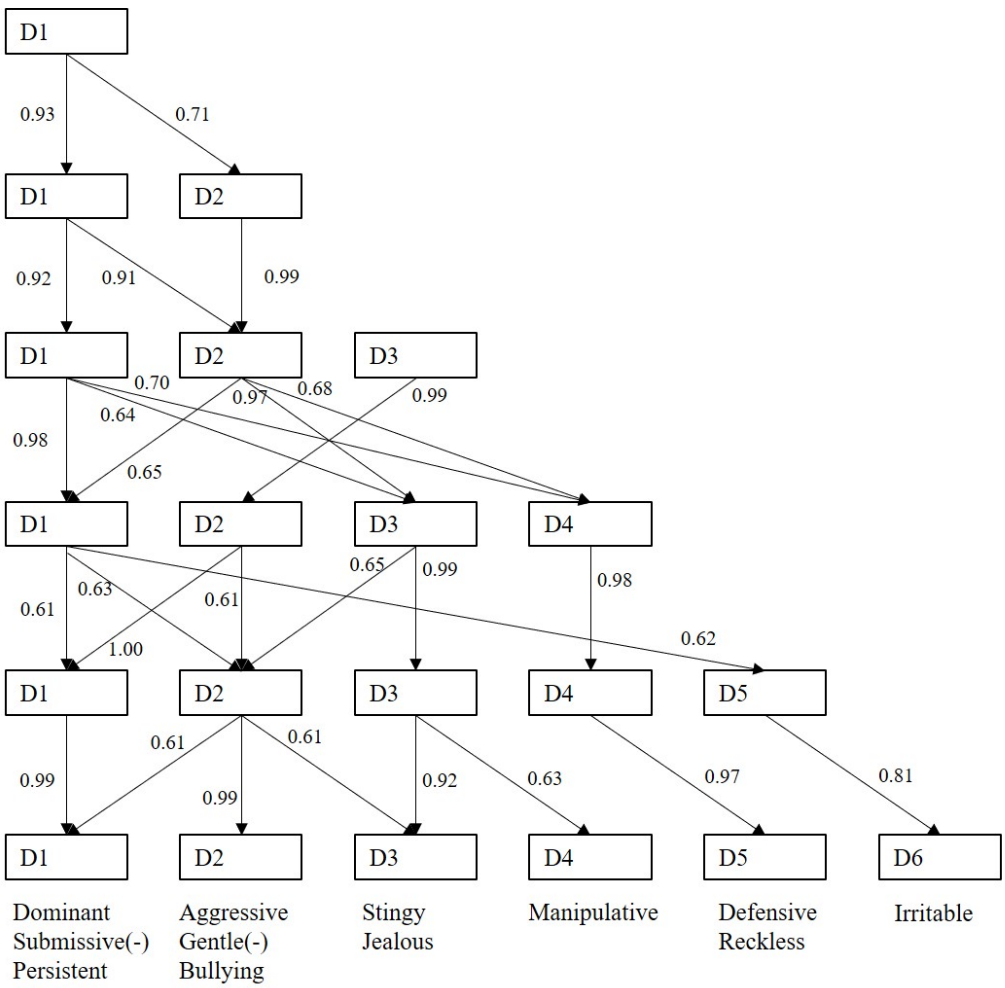

Figure 2.4: Oblimin-rotated factor diagram of items contained within the dominance factor in orangutans as measured by the OPQ. This diagram shows the development of the factor structure over successive iterations of increasing factor size. Associated items are listed under their respective facet. Loadings of less than 0.60 were excluded for clarity.

Table 2.21: Orangutan Neuroticism

Item	Facet	Loading
Impulsive	$N_{Or}1$	.88
Excitable	$N_{Or}1$	.70
Erratic	$N_{Or}1$	.65
Predictable(-)	$N_{Or}1$	.63
Stable(-)	$N_{Or}2$	.74
Timid	$N_{Or}2$	.73
Fearful	$N_{Or}2$	.69
Cool(-)	$N_{Or}2$	.64
Anxious	$N_{Or}2$	.57
Vulnerable	$N_{Or}2$	.45
Cautious	$N_{Or}3$	.80

Table 2.22: Orangutan Agreeableness

Item	Facet	Loading
Friendly	$A_{Or}1$	.92
Sociable	$A_{Or}1$	.88
Affectionate	$A_{Or}1$	.78
Sympathetic	$A_{Or}2$	.80
Protective	$A_{Or}2$	.80
Helpful	$A_{Or}2$	.62
Sensitive	$A_{Or}2$	.49

Table 2.23: Orangutan Intellect

Item	Facet	Loading
Independent	$I_{Or}1$	1.00
Dependent(-)	$I_{Or}1$	.69
Decisive	$I_{Or}1$	.49
Disorganised(-)	$I_{Or}2$	.74
Clumsy(-)	$I_{Or}2$	.52
Intelligent	$I_{Or}2$	.99

Table 2.24: Gorilla Sociability

Item	Facet	Loading
Helpful	$S_{Go}1$	.82
Sympathetic	$S_{Go}1$	.59
Sociable	$S_{Go}2$	.95
Friendly	$S_{Go}2$	.57
Dependent	$S_{Go}3$	.74
Affectionate	$S_{Go}2/S_{Go}4$	.36
Protective	$S_{Go}5$	.63

Intellect The six items of the orangutan intellect are split between three facets. Independent, low Dependent, and Decisive are connected to one ($I_{Or}1$), Disorganised and Clumsy to another ($I_{Or}2$), while the third contains only Intelligent.

2.3.4 Gorillas

Sociability The factor of sociability is divided into five facets. The first two facets contain two items each, Helpful and Sympathetic ($S_{Go}1$) and Sociable and Friendly ($S_{Go}2$). The other three items of Dependent, Affectionate, and Protective are all part of single-item facets.

Dominance Except for the item Defiant which does not load onto any facet, dominance contains ten facets. Only $D_{Go}3$ (Aggressive and Bullying) and $D_{Go}7$

Table 2.25: Gorilla Dominance

Item	Facet	Loading
Dominant	$D_{Go}1$	.79
Submissive(-)	$D_{Go}2$	.93
Aggressive	$D_{Go}3$	.84
Bullying	$D_{Go}3$	.59
Jealous	$D_{Go}4$	.90
Stingy	$D_{Go}5$	.52
Gentle(-)	$D_{Go}6$	.51
Cautious(-)	$D_{Go}7$	.61
Timid(-)	$D_{Go}7$	.58
Persistent	$D_{Go}8$	.87
Manipulative	$D_{Go}9$	.73
Irritable	$D_{Go}10$	.77
Defiant		

Table 2.26: Gorilla Emotionality

Item	Facet	Loading
Excitable	$E_{Go}1$	.86
Unemotional(-)	$E_{Go}1$	.52
Cool(-)	$E_{Go}2$	.99
Fearful	$E_{Go}3$	.76
Stable(-)	$E_{Go}3$	.49
Independent(-)	$E_{Go}3$	.40

(Cautious and Timid) contain more than one item while the other eight facets have a single item each.

Emotionality The factor Emotionality is made up of three facets. The first facet ($E_{Go}1$) is made up of Excitable and the reverse scored Unemotional. The second ($E_{Go}2$) is only made up of the item Cool and the final facet ($E_{Go}3$) is made up of Fearful and the reverse scored Stable and Independent.

Negative Affect The six items of Negative Affect are also divided into three similarly sized facets (Fig. 2.5). The largest of the three, $N_{Go}1$, consists of the

Table 2.27: Gorilla Negative Affect

Item	Facet	Loading
Anxious	$N_{Go}1$	.78
Erratic	$N_{Go}1$	.66
Autistic	$N_{Go}1$	.50
Vulnerable	$N_{Go}2$	1.00
Solitary	$N_{Go}3$	.85
Depressed	$N_{Go}3$	.53

Table 2.28: Gorilla Openness

Item	Facet	Loading
Lazy(-)	$O_{Go}1$	.81
Active	$O_{Go}1$	.58
Inquisitive	$O_{Go}2$	.92
Curious	$O_{Go}2$	.62
Innovative	$O_{Go}3$	.51
Inventive	$O_{Go}4$	.85
Individualistic	$O_{Go}5$	.50
Imitative	$O_{Go}6$	.71
Playful	$O_{Go}6$	.51
Conventional(-)	$O_{Go}7$	.68

items Anxious, Erratic, and Autistic and the smallest, $N_{Go}2$ contains only Vulnerable. The last facet in the domain ($N_{Go}3$) is made up of Solitary and Depressed.

Openness Openness as defined in gorillas is made up of seven facets. There are three multi-item facets which are represented by the negatively scored Lazy and Active ($O_{Go}1$), Inquisitive and Curious ($O_{Go}2$), and Imitative and Playful ($O_{Go}6$). The other four items of Innovative, Inventive, Individualistic, and the reverse scored Conventional are all single-item facets.

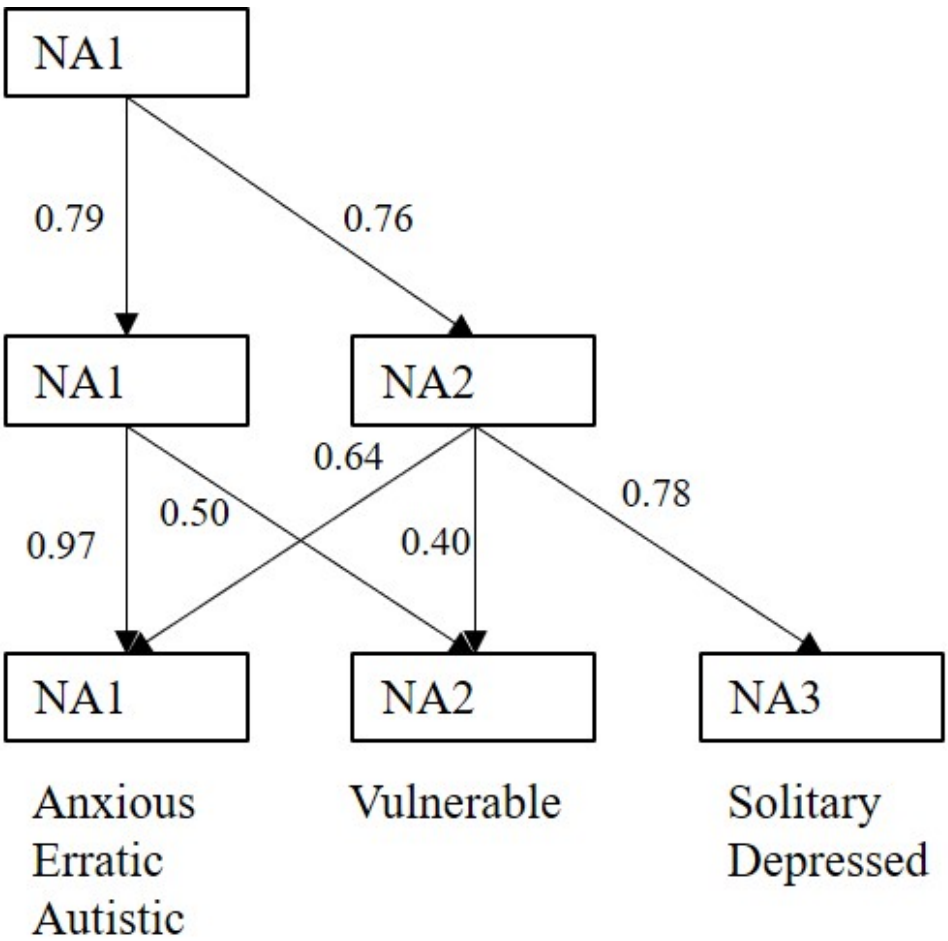

Figure 2.5: Oblimin-rotated factor diagram of items contained within the negative affect factor in gorillas as measured by the HPQ. This diagram shows the development of the factor structure over successive iterations of increasing factor size. Associated items are listed under their respective facet. Loadings of less than 0.40 were excluded for clarity.

Table 2.29: Gorilla Conscientiousness

Item	Facet	Loading
Disorganised(-)	$C_{Go}1$	.84
Clumsy(-)	$C_{Go}1$	.83
Thoughtless(-)	$C_{Go}1$	.52
Distractible(-)	$C_{Go}1$	.41
Unperceptive(-)	$C_{Go}2$	1.00
Intelligent	$C_{Go}3$	1.00
Reckless(-)	$C_{Go}4$	.91
Predictable	$C_{Go}5$	.52
Sensitive	$C_{Go}5$	.38
Decisive		

Conscientiousness There are five facets that make up the factor of conscientiousness. The first and largest facet ($C_{Go}1$) consists of Disorganised, Clumsy, Thoughtless, and Distractable. The other multi-item facet in this factor is $C_{Go}5$ which is made up of Predictable and Sensitive. The final three facets are single items and contain Unperceptive, Intelligent, and Reckless. The final item, Defiant, is not represented by any facet.

2.4 Discussion

For most factors analysed in these species, we see a clear facet structure within the domains. These facets reveal a number of interesting similarities as well as key differences amongst these apes.

2.4.1 Chimpanzees

In both the CPQ and HPQ in chimpanzees we can see roughly similar facets structures, modified of course by the addition of extra items in the HPQ. In extraversion we see some strong consistent facets involving the items Active,

Playful, and Lazy (E1 and $E_{Ch}5$) as well as a grouping of Sociable, Affectionate, and Friendly (E2 and $E_{Ch}3$). These fit fairly well with the proposed facets in King et al. (2008). The two facets in that study were created by dividing items into groups based on whether they were related to physical activity or social behaviour, which coincided with the definitions used for two of the facets which make up human extraversion (Costa & McCrae, 1995a). While Playful seems to be more strongly associated with Active and low ratings on Lazy, the physical activity facet defined by King et al. (2008), the remaining item allocations largely fit with their facet composition. The other main difference here is the number of facets and the further detail given in the separation of facets like $E_{Ch}4$ (Solitary and Depressed) and single-item facets like E5 (Imitative) from the larger grouping of social behaviours.

Conscientiousness showed some larger differences between the two questionnaires which is not surprising considering that the number of items increased by nearly 50% from the CPQ to the HPQ. The most consistent facet seems to be C2 (Irritable and Aggressive) in the CPQ and $C_{Ch}1$ (Aggressive, Defensive, Jealous, and Irritable) in the HPQ. The addition of the new HPQ items seems to have also drawn enough variability to separate out several items that were previously part of multi-item facets in the CPQ facets into their own single item facets, which also was the case for most of the new items. Two points from the HPQ analysis provide some areas for concern as to the true overall structure. With nine facets present, Reckless (which is contained in its own facet in the CPQ) is left orphaned without loading on any facet greater than the 0.30 cut-off. There is also a facet, ($C_{Ch}5$), which only has a small negative loading (the only primary negative loading seen in any facet in this study) on Predictable. Given this, it is possible that this analysis has overestimated the number of

strong facets for fewer than nine facets for chimpanzee conscientiousness.

At nine and fourteen facets respectively, chimpanzee dominance as measured by the CPQ and HPQ possess the two highest number of facets seen in this study (tied with the nine facets of CPQ conscientiousness). These facets also tended to be quite small, with D4, D7, and D8 consisting of two items and the remaining facets in both scales being made up of only one item each. In the HPQ the item Manipulative is also not accounted for by any of the existing facets.

Neuroticism and Openness to Experience suffer from the same problem of low item representation in both scales used here. While in the NEO-PI-R (Costa & McCrae, 1992) used in humans there are 48 items per factor and eight per facet, Neuroticism in the CPQ contains three items while the HPQ contains four and Openness is represented by only two items in the CPQ and four in the HPQ. It is still, however, possible to derive facets from these scales though the number of facets is limited by the number of items. In Neuroticism, only one facet exists in the CPQ but with the addition of Cool and the redistribution of Unemotional and Autistic in the HPQ two facets emerge. Conversely, the addition of two new items to openness from the CPQ to the HPQ did not change the single facet and all four items (Inventive, Inquisitive, Innovative, and Curious) were not divided.

Agreeableness was bolstered by the additional item Conventional from the HPQ and this changed the facet structure quite a bit. In the CPQ two facets were identified, one that contained only the item Gentle and another that incorporated the remaining four items (Protective, Helpful, Sympathetic, and Sensitive). In the HPQ, the new item Conventional joined the facet with Gentle while A1 was broken into three facets, $A_{Ch}4$ with Protective and Sensitive and

two single item facets with Helpful and Sympathetic.

2.4.2 Bonobos

Though using the same HPQ as the chimpanzee data, bonobo personality factors differ in both composition and meaning from their *Pan* cousins. However there are still some similarities in facet composition where the same items group together. The extraversion facet as defined in bonobos contains only four items compared to the chimpanzee extraversion's ten. These break down into two facets, $E_{Bo}1$ with Solitary and Depressed, which mirrors $E_{Ch}4$ and a single-item facet with Autistic. The last item associated with this factor, Individualistic, does not load above the threshold of 0.3 for any facet and is not represented. Looking back at Weiss and King (2015) again (though they did not include bonobos in their study), we see that their initial sorting of items into physical activity and social aspects would be impractical here as elements of the former are associated with Openness in bonobos. This is not meant to be a criticism of their study, which defines the facets they used quite appropriately as seen in this analysis, but as a confirmation of the usefulness of the present methodology in determining hierarchical personality structure above and beyond a priori theoretical characterisations.

Conscientiousness contains the highest number of facets in the bonobo structure at eight. Three of these, $C_{Bo}1$, $C_{Bo}2$, and $C_{Bo}4$, are made up of two items while the rest are single-item. Though containing several items present in chimpanzee conscientiousness, when comparing between the two species we should also look at the attentiveness factor as well. A large part of attentiveness is made up of items that are associated with high conscientiousness in chimpanzees while the rest are comprised of high chimpanzee dominance

items. This factor breaks down into four facets, two multi-item and two single-item. When we compare the items that do co-occur within these facets we see several differences in association. While Aggressive and Irritable stay together with Defensive and Jealous in $C_{Ch}1$, in bonobos these four items split apart. Defensive and Jealous break off into their own facets and Irritable and Aggressive pair off with Erratic and Bullying in $C_{Bo}1$ and $C_{Bo}4$. Another notable difference in bonobo conscientiousness is the combination of Stingy and Manipulative. Both items are included in chimpanzee dominance but here we see them remain separate, with Stingy falling into its own facet and Manipulative not being represented by any facet. The items which make up the two multi-item facets in attentiveness are all contained and kept separate in chimpanzee conscientiousness with the item Unperceptive (defined by a single-item facet in attentiveness) substituted for Disorganised in $At_{Bo}3$.

In agreeableness, there is quite a difference between bonobos and chimpanzees both in item and facet composition. Of the four items which overlap the two, Helpful and Sympathetic are together in the only multi-item facet $Ag_{Bo}1$ with Friendly and Affectionate while they are separate in $A_{Ch}1$ and $A_{Ch}2$. The opposite is true for the other two shared items, Protective and Sensitive, which make up $A_{Ch}4$ together and $Ag_{Bo}3$ and $Ag_{Bo}4$ independently.

Openness to experience is much more widely represented in bonobos as far as the number of items is concerned and several items representing physical activity in chimpanzee extraversion are contained herein. Though quite robustly associated with the same facet in chimpanzees ($E_{Ch}5$), Active, Playful, and the negative aspects of Lazy are all a part of different facets in bonobo openness. Innovative and Inventive stayed a part of the same facet ($O_{Bo}3$) but Inquisitive and Curious have broken away into their own facets compared to $O_{Ch}1$.

While no neuroticism factor exists in bonobos, three of the four items associated with this factor in chimpanzees are contained within the bonobo factor of Assertiveness which also includes several aspects of dominance. This is reflected in $As_{Bo}3$ which contains these three items (though in chimpanzee neuroticism Excitable is scored in the opposite direction and associated with $N_{Ch}2$ instead of $N_{Ch}1$). The second large facet, $As_{Bo}5$, is made up of Fearful, Timid, Anxious, and Vulnerable which are all present and part of single-item facets in chimpanzee dominance. The same goes for Dependent and Independent in the last multi-item facet $As_{Bo}5$.

2.4.3 Orangutans

Looking again at the facets used in Weiss and King (2015), we see that their factor compositions were not too far afield. The first facet $E_{Or}1$ does seem to be representative of aspects of physical activity, though with the additional inclusion of the item Imitative, which they attributed to the facet "Gregariousness." This second facet on the other hand does not seem to be represented particularly well by the items selected. We see Playful combined instead with Unemotional ($E_{Or}2$) and the items Depressed and Solitary in their own single-item facets. The combination of Activity and the negative loading Lazy appears to fit well in the association in the chimpanzee facet $E_{Ch}5$ though Playful does split off into $E_{Or}2$. Inquisitive and Curious ($E_{Or}3$) seem to fall closer to chimpanzee structure as well. Though they are included in openness in both chimpanzees and bonobos, the former includes them in the singular openness facet while they are single-item facets in the latter. The combination of negatively loaded Conventional and Inquisitive ($E_{Or}4$) seems to be a bit more of a unique relationship to orangutans as they are separate facets within bonobo

openness and associated with different factors in chimpanzees.

When looking at dominance, we can immediately make our blanket comparison with chimpanzee dominance and its lack of multi-item facets. The exception being Manipulative which has no facet in chimpanzees and is a single-item facet in orangutans. In comparisons with bonobos however, we find very similar misalignments in the factors containing these sets of items. The first facet ($D_{Or}1$) contains Dominant, Persistent, and negative Submissive, all of which are separate facets within bonobo assertiveness. Much the same situation presents itself with facet $D_{Or}2$ only this time Aggressive and Bullying are single-item facets within bonobo conscientiousness while Gentle is positively loaded and in facet $C_{Bo}8$ with Predictable. $D_{Or}3$ (Stingy and Jealous) is also split in bonobos between $C_{Bo}5$ (Defensive and Jealous) and $C_{Bo}7$ (Stingy and Manipulative) while the last multi-item facet $D_{Or}5$ is divided between $C_{Bo}5$ and $C_{Bo}6$ (Reckless).

Neuroticism in orangutans divides into two large and one single-item facet. The first contains Impulsive, Excitable, Erratic, and the reverse scored Predictable ($N_{Or}1$). In chimpanzees these items have no strong relation to each other, three are single facets in conscientiousness while Excitable is part of $N_{Ch}2$. In bonobos, which have no defined neuroticism factor, Impulsive, Erratic, and Predictable are also associated with conscientiousness with Excitable making up a part of $As_{Bo}3$ as a negatively loaded item with Stable, Cool, and Decisive. This facet is closer to the inverse of $N_{Or}2$ which also contains Timid, Fearful, and Anxious, which in chimpanzees are all single-item facets in dominance. The last facet is solely Cautious, also a single-item chimpanzee dominance facet and not strongly associated with any factor in bonobos.

The agreeableness factor in orangutans is split more or less down the middle

into two facets; Friendly, Sociable, and Affectionate ($A_{Or}1$) and Sympathetic, Protective, Helpful, and Sensitive ($A_{Or}2$). The first has similarities with $Ag_{Bo}1$, though Sociable is a part of $Ag_{Bo}2$, and is identical to $E_{Ch}3$. The second shares items with the other half of $Ag_{Bo}1$ (specifically Helpful and Sympathetic) and $Ag_{Bo}2$ (Sociable) and $Ag_{Bo}3$ (Protective). In chimpanzees, these items are split between three of the four agreeableness facets, $A_{Ch}1$ (Helpful), $A_{Ch}2$ (Sympathetic), and $A_{Ch}4$ (Protective and Sensitive).

Though unique amongst the great ape personality structures, intellect nevertheless has similarities with facets in other domains in *Pan*. The first intellect facet, $I_{Or}1$ consists of Independent, negative Dependent, and Decisive. The first two items mirror $As_{Bo}5$ while Decisive is instead a part of $As_{Bo}3$. In chimpanzees these are all included in the plethora of single-item dominance facets. The second facet of Disorganised and Clumsy ($I_{Or}2$) is the same as $At_{Bo}3$ and the items contained within are split in chimpanzee conscientiousness with Clumsy paired up with Unperceptive in $C_{Ch}4$ and Disorganised on its on in $C_{Ch}6$. In an interesting turn of full consistency, the final facet of only Intelligent is also in its own facet in chimpanzee dominance and in bonobo attentiveness.

2.4.4 Gorillas

The factors identified in captive gorilla personality also differ somewhat from those seen in other apes but several meaningful parallels exist. In the factor of sociability, we see the items Helpful and Sympathetic combining together in facet $S_{Go}1$. We see these items grouping together with Friendly and Affectionate in Bonobo $Ag_{Bo}1$ but remaining separate at the facet level when they appear in the same factor in both orangutans and chimpanzees when using the

HPQ. In the CPQ these stay together as well in the large multi-item agreeableness facet A1 which makes up most of the factor. The other larger factor in sociability is $S_{Go}2$ containing Sociable and Friendly. These two items are paired in orangutans ($A_{Or}1$) and in both measures of chimpanzee personality (E2 and $E_{Ch}3$) but are in different facets in bonobo agreeableness.

Dominance seems to follow the larger trend of relatively separate items with its ten facets for thirteen items. We see a similar pattern especially in chimpanzee dominance with three multi-item facets in the CPQ data ($D_{Ch}4$, $D_{Ch}7$, and $D_{Ch}8$) and none in the HPQ. Here we see the combination of the items Aggressive and Bullying ($D_{Go}3$), which are also together in orangutans ($D_{Or}2$) and bonobos ($C_{Bo}4$), and the items Cautious and Timid ($D_{Go}7$) which are together in the same facet only in chimpanzees when using the CPQ (D4).

Emotionality, unique to captive gorilla personality, contains three facets. The first ($E_{Go}1$), Excitable and low Unemotional, only appear together in the solitary facet N1 seen in chimpanzee CPQ neuroticism. The other multi-item facet, Fearful, low Stable, and low Independent ($E_{Go}3$), is a wholly unique combination.

Negative affect is another domain unique to gorillas and has two multi-item facets out of three total. The facet $N_{Go}1$ (Anxious, Erratic, and Autistic) does not have a clear parallel in the personality structure of any of the other species examined in this study but the third facet, $N_{Go}3$ (Solitary and Depressed) does have partners in chimpanzee extraversion ($E_{Ch}4$) and bonobo extraversion ($E_{Bo}1$) but are separated in orangutan extraversion.

In openness, we see another instance of one of the stronger associations across the facet structures between the items of Active and the reverse scored Lazy ($O_{Go}1$). This is a combination we also see in orangutans with Imitative

($E_{Or}1$), and in both chimpanzee measures with playful (E1, $E_{Ch}5$), though interestingly they are separated within bonobo openness. These other two items in gorillas are combined to form the second multi-item facet ($O_{Go}6$) while the last is represented by the items Inquisitive and Curious ($O_{Go}2$) which also appears in orangutans ($E_{Or}3$) and in the chimpanzee monolithic openness facet $O_{Ch}1$ for the HPQ (Curious was not one of the original 43 CPQ items) but not in bonobo openness where they are both single-item facets.

The ten conscientiousness items in the domain as it is defined in gorillas can be broken down into five facets. The largest by half, $C_{Go}1$ (Disorganised, Clumsy, Thoughtless, and Distractable), has similarities to orangutan $I_{Or}2$, though this scale did not include Thoughtless or Distractable. We also see these items combined in the two bonobo multi-item attentiveness facets $At_{Bo}1$ (Thoughtless and Distractable) and $At_{Bo}2$ (Clumsy and Disorganised) though none of them appear together in chimpanzees when using either the CPQ or the HPQ. Predictable and Sensitive ($S_{Go}1$) do not group into the same factor in orangutans, bonobos, or chimpanzees and so is somewhat of a unique facet. Notably Intelligent here as well occupies its own single-item factor, completing the set amongst all of the nonhuman great apes as disassociated at the facet level from any other items.

2.4.5 Facets as a whole in nonhuman apes

These facets and the parallels and divergences between the subject species provides clear evidence of the structure underlying the domain-level composition of personality in nonhuman great apes. The majority of facets are clear, have high positive loadings, and have limited cross-loading and ambiguity.

The major exceptions regarding the clarity and brevity of these structures

however, are those factors with a high number facets and many facets which are represented by only one item. The clearest example of this is dominance in chimpanzees with fourteen facets covering fifteen items with one item left unrepresented. To use these facets in a predictive analysis, for example correlating with mortality or well-being, would be little different that simply using individual items. This may not be as unreasonable as it sounds for item-level analysis has been shown in humans to be valid and highly useful in looking for specific correlates of outcomes (Mõttus et al., 2017, 2018).

In this study we have not assigned semantic labels to our facets. The purpose of this is, as stated above, to avoid giving undue heuristic meanings to these facets beyond their actual statistical construct definitions. Instead we have used a numbering system to distinguish amongst species and factors. The fact that many of the facets identified here consist of only one item reinforces the value of our decision as it would become increasingly difficult to assign independent yet memorable and easily identifiable labels to these facets without confusing them with the items they represent, a subtle but important distinction.

Nonhuman personality at a factor level has already been used to great effect in studies of health outcomes (Altschul et al., 2018), welfare (Robinson et al., 2016), well-being (Weiss et al., 2002, 2006), and more. The additional use of facets in these studies can provide a more detailed and specific approach. Facet analysis often produces fewer but stronger associations between specific aspects and can provide greater specific predictive utility. An example of this in humans is the relationship between certain personality facets and body mass index (BMI, Terracciano et al., 2009). Here, low Conscientiousness was associated with being overweight or obese but this association was driven by low

scores on the Order and Self-Discipline facets and, while there was a strong association with the Neuroticism facet Impulsiveness, there was no overall association with Neuroticism on a factor level. It is associations like these that are easily missed while maintaining a broad perspective and have great potential predictive capability and applied usage.

One potential limitation of this study is the representativeness of the subjects. All samples were collected from captive animals housed in zoos, sanctuaries, and research institutions. The problems with this have been highlighted by Boesch (2007) and, while much more relevant to experimental studies of great apes than personality assessments, concerns may still be raised about the generalisability of these findings.

This may not be as detrimental as it first appear however. By and large human beings also do not live in the same types of environments as they did tens or hundreds of thousands of years ago (Sterelny, 2011). Most humans participating in psychological research have ready access to food, a peaceful and stable social group, limited and predictable daily ranges, and constant exposure to other people and potentially stressful events and circumstances (Tomasello, 2009). By this definition, it is potentially *more* appropriate to compare most modern humans to captive nonhuman apes than it is to compare them to wild counterparts.

In any case, it is prudent to compare personality data from wild and captive animals of the same species to assess if there are any inherent differences between the two groups. In fact when data from wild and captive bonobos are compared we do see a difference in the personality structure and factor composition (Weiss et al., 2015; Garai et al., 2016). There is the potential for alternative explanations for these differences, however, in that a large number

of items were left out of the factor analysis. This resulted in a less stable structure of the factors and would benefit from further validation.

One oft-repeated criticisms of research investigating personality in nonhuman animals is the idea that the methods used to collect data are unsound. The argument stems from the fact that nonhuman personality research relies heavily on observer report data. This data, it is suggested, does not actually represent any true constructs or variability in the animals observed but merely is a measurement of anthropomorphising on the part of the observer (Uher, 2008a; Wynne, 2004), ascribing undeserved human-like traits to animals or objects. These concerns have been shown to be unwarranted however, with personality dimensions in chimpanzees and orangutans being replicated when differences between rater means and rater-item interactions had been removed from ratings and different when analysing items from which differences between animal means and animal-item interactions had been removed (Weiss et al., 2012). In short, raters did not show a species-level bias for certain traits (as would be expected if they had preconceived notions about the species behaviour) and ratings of individual animals on items did vary from the mean (meaning that individual animals' were not just given a "personality" score but each item was assessed independently).

2.4.6 Future Study

The universal goal of replication in psychology can also unsurprisingly be applied here. Using this method of facet analysis as a starting point, independent verification of these facets using the same methods on different data and using novel methods independent of factor analysis would strengthen our conclusions here and provide a more robust base for facet-level research.

The simplest expansion of this study is in depth and breadth. These methods for deriving facets can easily be applied to any number of species that have a factor structure of personality. This expansion would confer the same specificity and advantages in predictive utility provided by these finer analytic tools to these other species. It would also facilitate growth in both the study of personality correlates within these new species by providing a method for analysing multi-level factor structure as well as clearing more ground for detailed comparative research between them.

It may be that facets are in fact not the most useful level of the personality hierarchy to use in future studies. In some instances, particularly in dominance as it is defined in chimpanzees by the HPQ, we see that these facets are all defined by single items anyway. It has been shown that in human personality, analysis on the level of single or pairs of items can produce meaningful results (Mõttus et al., 2017, 2018). These "nuances" (McCrae, 2015), as they are known, provide value in their specificity. When using this hierarchical level of personality as a predictor for other otcomes, many of these items will not correlate significantly with the aspect being studies, often only a few will have any connection at all. These few items however, controlling for multiple comparisons and other concerns, tend to have vastly increased predictive utility in the area being studied. Future work investigating lower-order hierarchical personality structure in nonhumans should apply this idea and look at whether this item-level analysis may be better suited to accomplishing the goals of this study and beyond the specificity added by the facets identified here to the factor-level associations.

We have at several points extolled the value of data-derived facets over theoretically imposed facets. Indeed when comparing our facets with those

used in Weiss and King (2015), most are the same but some, in particular their use of orangutan Gregariousness, do not fit well with our findings. It would make sense then that we should seek to bolster our facet structure claims using further data-driven work. One potential method in particular that may be useful to verify our findings is a spectral cluster analysis. Here, data are mapped in n-dimensional space and associations are determined by proximal distance in this space. This has been used in personality research previously by Brocklebank, Pauls, Rockmore, and Bates (2015) to compare the Five-Factor Model to the HEXACO of personality and indeed some differences did occur. Future work on these hierarchical levels should also focus on multi-method analysis to confirm findings and lend strength to the assertions of their validity as independent constructs rather than artefacts of analytical techniques.

Overall, this study provides evidence for the existence and composition of lower-order hierarchical personality structure in several nonhuman great apes. These facets share several similarities between species but by and large are, like their overarching factor structure, unique to each species. These facets have the potential to be useful in the investigation of personality correlates, providing an increased specificity for predictors and finer tools to use in expanding the utility of personality in nonhuman primates.

Chapter 3

A nuanced look at personality development in chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), orangutans (*Pongo spp.*), and gorillas (*Gorilla spp.*)

3.1 Introduction

The factor structures of adjectives related to personality has been a subject of research since 1934 (Thurstone, 1935). Thurstone's factor analysis of observer ratings of university students on 60 descriptors established a five-factor structure but this line of inquiry was not followed through and it took decades of work on the lexical approach to personality theory by figures such as Allport and Odbert (1936) and R. B. Cattell (1943) to arrive at the idea of a hierar-

chical organisation of these factors.

Warren Norman, drawing from Tupes and Christal's (1961) study of the effectiveness of officers in the United States Air Force, suggested that there may be multiple orders of categorisation of personality descriptors (Norman, 1967). He concluded that there were three levels of personality. At the basic level are the specific responses to specific situations, organised at the second level into habits, dispositions, etc. The third level further collapses these into broader groups of characteristics and finally at the top are the five factors representing the highest reduction and generalisation.

Personality research, especially trait theory, fell out of favour in the late 1960's and 1970's (Digman, 1990) and was only brought back into the light in the 1980's thanks to psychologists like Lewis Goldberg (1990) who revived the lexical approach and trait theory. Here as well were the beginnings of our modern conception of the five-factor theory and the quintessential tool, the NEO-PI (Costa & McCrae, 1985). Development of this scale continued and the revised version (NEO-PI-R, Costa & McCrae, 1992) is widely used today (Dwan & Ownsworth, 2019). Costa and McCrae also set out the hierarchical nature of their scale, defining and validating facets (Costa & McCrae, 1995a), and later suggesting the wider use of the even more fundamental item or nuance level (McCrae, 2015).

3.1.1 The Personality Hierarchy

The Five-Factor Model, being a hierarchical structure organises multiple levels of personality traits. The most common of which being facets (McCrae & Costa Jr, 1992). Each of the five factors was divided into six facets based on past theory and measurement and items were chosen for each facet to maximise

distinction from and comparability to other facets (Costa & McCrae, 1995a). These facets have since been utilised in several studies (e.g. Costa et al., 2014; McCrae & Costa, 1997a) and have provided a useful basis for comparison the study of job performance (Judge et al., 2013), personality disorder diagnoses (Reynolds & Clark, 2001), and specific behaviours (Paunonen & Ashton, 2001).

More recently, McCrae (2015) and Mõttus et al. (2017) proposed that a further lower order could exist. These "nuances" consist of single items or couplets of closely related items. As an example, the items "bitterness" and "touchiness" may be nuances of the "angry hostility" facet of Neuroticism. As a general definition, these nuances identify either the eliciting situation (such as a fear of heights being a source of anxiety) or characteristic response to a range of situations (such as a nervous tic as an expression of internal anxiety). The concept of nuances first came about as a potential explanation for the greater predictive ability of retest reliability compared to internal consistency when looking at the differential stability, consensual validity, and heritability of facet scales (McCrae, Kurtz, Yamagata, & Terracciano, 2011). In particular, this was applied to the five-factor model by McCrae (2015), who proposed that the explanation for this discrepancy could be due to the reflection in retest reliability of "both the variance common to items in a facet scale and the item-specific variance that distinguishes different nuances of the same facet". In this way he suggests that the better conceptualisation of traits is "as the union, rather than an intersection, of their subtraits."

Some of the main proponents for the use of nuance-level analyses are Mõttus and colleagues (2017, 2018). They argue that these nuances can provide specific and much greater predictive power than broader, higher-order traits such as factors or even facets. To support this they outline three criteria that should

be met if we are to give any weight to item-level analysis beyond its potential for "p-hacking" (Head, Holman, Lanfear, Kahn, & Jennions, 2015).

These criteria are taken from Five-Factor Theory (McCrae & Costa, 1999) and state that these traits must be "detectable by different observers, stable over substantial periods of time, and have some demonstrable genetic foundation." (Mõttus et al., 2017). Furthermore, for these items to be considered as their own level in the trait hierarchy, they must show this consensual validity, stability, and heritability above and beyond that shared with facets.

To test personality nuances against these criteria, Mõttus et al. (2017) used cross-sectional and longitudinal data from the Bielefeld Longitudinal Study of Twin Adults (BilSAT; Kandler et al., 2013) and from data collected from the Estonian gene bank (Vainik, Mõttus, Allik, Esko, & Realo, 2015). Looking at consensual validity, they found that there was significant agreement between item residual scores from self- and observer- report personality questionnaires with the common variance of the facet removed (Mõttus, McCrae, Allik, & Realo, 2014; Mõttus et al., 2017).

Rank-order stability of the nuances was assessed by examining retest scores from a group of individuals at a five year interval. Mõttus et al. (2017) found that there was demonstrable trait-like stability at the nuance level that was comparable to other orders of personality traits.

Heritability was assessed by comparing twin pairs in several genetic models. Overall, little evidence of shared environmental effects was found and variability was primarily influenced by genetic and nonshared environmental factors. This is largely consistent with genetic analyses of other trait levels and supports the idea that nuances have a basis in biology. Mõttus et al. (2017) also point out that to have any use as a hierarchical level, there should be demo-

graphic variation and predictive utility. This may be self-evident but if these observed variations are limited to a small subset of the population and are not generalisable or if they have no correlates with other aspects of life then there would be little value in studying them in depth, especially when attempting to apply them to the population at large.

Mõttus et al. (2017) concluded that, taken together, this evidence supports the idea that nuances exist as a temporally stable, consensually valid, and heritable lower-order set of traits in human personality and that they can be used to predict important outcomes in conceptually meaningful ways. The next step lies in the application and utility of item-level traits, to increase depth of understanding, to an area that is rapidly expanding the breadth of personality research: personality in nonhumans.

3.1.2 Personality in Nonhumans

Personality as a concept in nonhuman animals has been around since at least 1925 when Köhler (1925) described individual differences in his chimpanzee subjects as "personality". The modern conceptualisation of a hierarchical factor structure of personality, however, was sparked by Stevenson-Hinde and Zunz (1978); Stevenson-Hinde et al. (1980b, 1980a) in the late 1970's. This idea of questionnaire measurement of personality in nonhuman animals was then later taken up by King and Figueredo (1997). They began to construct a questionnaire to measure personality in chimpanzees in the same way Costa and McCrae developed the Five-Factor Model (Costa & McCrae, 1986). Using a set of adjectives from Goldberg's lexical studies (1990) and two extra items, they developed a 43-item observer-report questionnaire that could be used to collect data on chimpanzee personality. The Chimpanzee Personality Questionnaire

(CPQ) data was then factor analysed to reveal a six-factor structure that was able to be rated reliably by observers (King & Landau, 2003), maintained rank-order stability with age (King et al., 2008; Weiss & King, 2015), was consistent across several chimpanzee groups (King et al., 2005; Weiss et al., 2007) and through human cultural differences and translations (King et al., 2005; Weiss et al., 2009), and not influenced by anthropomorphic biases (Weiss et al., 2012). Five of the chimpanzee factors identified were broadly similar to the human five factors and were given the same names. The sixth factor, indicating an individual's propensity to exhibit dominant behaviour in social situations with conspecifics, was labelled Dominance. Later, nine items were added to the questionnaire (King et al., 2006) and the subsequent Hominoid Personality Questionnaire (HPQ) has been adapted and applied to a wide range of species from Bonobos (Weiss et al., 2015) to deer (Bergvall et al., 2011).

Application of the HPQ to different species revealed that each species has its own personality structure with a different number and composition of traits. For example, bonobos have the same number of factors as chimpanzees but the composition is different (Weiss et al., 2015) and wild mountain gorillas only have four factors (Eckardt et al., 2015). This variation in trait structure represents the effects of differential selective pressure on personality in these species (see Chapter 1).

In the same way that personality in humans can be used to predict health and life outcomes such as values and subjective well-being (Kandler, Zimmermann, & McAdams, 2014), personality in nonhumans can be used to predict similar outcomes. Though some direct comparisons are difficult (such as prediction of values), health and well-being relationships with personality have been shown to exist in chimpanzees and other animals as well as in humans. In

both chimpanzees and humans high Agreeableness is associated with a longer lifespan (Altschul et al., 2018) and well-being shared a variety of connections to personality in several species (Weiss et al., 2002, 2006; Steel, Schmidt, & Shultz, 2008; Weiss et al., 2009; Weiss, Adams, & King, 2011; M. C. Gartner & Weiss, 2013).

3.1.3 Great Apes

Looking outward from humans in the evolutionary tree, the nearest branches hold the great apes. Going back 85 million years ago (mya), there was only one primate (Martin et al., 2007). After the mass extinction at the end of the Cretaceous period, ecological niches previously occupied by dinosaurs and other reptiles were soon filled with the explosively radiating mammal species, including primates. Leaping ahead to between 32 and 35 mya, the hominoids (more technically as the superfamily hominoidea and less technically as the apes) diverged from the rest of the primate taxa (Perelman et al., 2011; N. J. Stevens et al., 2013). From this original ape split off the lesser apes, today gibbons and siamangs (20 mya), and after that the great ape species known today and who, with one notable exception, make up the subjects of this study further diverged. Approximately 18.5 mya a group of apes found themselves in southeast Asia and began to develop into orangutans . Remaining in Africa, later divergences led to the modern species of gorilla (8.3 mya) and to the common ancestor of the genera *Pan* and *Homo* (6.6 mya). The latest species of the extant great apes to diverge were the chimpanzee and the bonobo. This separation occurred around 2.2 mya when one group of their common ancestors crossed the Congo River during one of its periods of low discharge and were subsequently isolated when the river later resurged (Takemoto et al., 2015).

As this speciation led to physiological and cognitive changes, so too did it allow for the divergence of personality traits. The unique personality structure of each of the great apes has developed over time in response to the evolutionary circumstances surrounding them. As such, we are able to use our knowledge of these circumstances along with the evolutionary distance between humans and other apes to paint a picture of how personality has developed in humans and what circumstances have shaped our personality as a species (McHenry, 1982). While some insight may be gained from preserved morphology (Lister, 2014) or through the fossil or archaeological record (Klein, 1995, 2000), at the moment comparative personality assessment is the most effective method available to us for assessing prehistoric personality (S. D. Gosling & Graybeal, 2007). These comparisons can give us clues as to when and under what circumstances modern human personality evolved (S. D. Gosling & John, 1999; de Queiroz & Wimberger, 1993).

Chimpanzees

Of the six personality factors identified in chimpanzees, the first and largest factor of dominance stands out as the greatest divergence from human personality. Distinct from the social dominance hierarchy, Chimpanzees with high levels of dominance tend to be rated as being better at making alliances with conspecifics, are more assertive and decisive, and possess better competitive social prowess than those with lower dominance scores (King & Figueredo, 1997; Weiss & King, 2007). It is important to note here that this divergence, and indeed other divergences amongst species, are not from the addition and removal of items from the questionnaire but rather a restructuring and a change in loadings amongst factors. For example, items like “timid” and “dominant”

that load on extraversion in humans and "cautious" and "fearful" that load on neuroticism have, in chimpanzees, been redistributed to dominance. Block (1995a) points out that these dimensions also are not "monolithic edifices" but can shift and modify in much more fluid on the item level.

The other five chimpanzee factors share labels and, generally, items and conceptual similarities with the Big Five in humans (King & Figueredo, 1997). As a whole these six factors have been described using both CPQ (King & Figueredo, 1997) and the HPQ (Weiss et al., 2009) and these measures have been shown to have high validity and reliability across several contexts (King & Landau, 2003; King et al., 2005; Weiss et al., 2007, 2012).

Bonobos

Bonobos also have six personality factors but these differ in their structural composition from the chimpanzee six factors. Four of these factors, extraversion, openness, conscientiousness, and agreeableness, correspond to the factors of the same names present in humans and in chimpanzees (Weiss et al., 2015). Another factor, attentiveness, is similar to the factor of attentiveness seen in brown capuchins (Morton et al., 2013) and comprises items that in chimpanzees are associated with high dominance and high conscientiousness (Weiss et al., 2009). The final factor, assertiveness, is similar to the chimpanzee dominance factor.

The discovery of a personality factor governing dominance further confirms humans as the only species of ape without a clear dominance factor (Digman, 1990; Goldberg, 1990; de Waal, 1995). It was possible that, in a more cooperative-egalitarian society that is thought be one of the driving factors behind human personality evolution (Boehm, 1999; Weiss, Adams, Wid-

dig, & Gerald, 2011), bonobos may no longer have the same selective pressures for dominance (Eckardt et al., 2015). This is largely due to the perception of bonobo society as far more egalitarian than chimpanzee society (de Waal, 1984, 1995), suggesting that there would be less selective pressure for features related to maintaining social dominance. The presence of a dominance factor in bonobos begins to resolve itself when we look at captive bonobos however. In captive animals we see evidence for a much stricter social dominance hierarchy that would support the emphasis on dominance (or more correctly assertiveness) in bonobo personality (J. M. G. Stevens et al., 2007; Vervaecke et al., 2000).

Another interesting development in bonobo personality research was a study by Garai et al. (2016) on a subset of 16 bonobos from a wild, habituated population in the Democratic Republic of the Congo. Here, only five factors were identified that differed from those previously observed. While this does differ from previous findings, the authors point out that there is the potential for a reduction in the stability of this structure due to a combination of several items being removed from the analysis due to low inter-rater reliability and the limited sample size (MacCallum et al., 1999; Velicer & Fava, 1998) and so these results should be interpreted with some measure of caution.

Orangutans

The genus *Pongo* continues the pattern of divergence from the genera of *Pan* and *Homo*. Orangutans have five personality factors, extraversion, neuroticism, agreeableness, dominance, and intellect (Weiss et al., 2006). The first three fit largely in the same mould as the eponymous traits in humans and chimpanzees and the dominance factor reflects that seen in chimpanzees. Intellect, however,

seems to largely straddle the line between high human conscientiousness and openness to experience, drawing in variance from items associated with both as well as a few others. What is more notable perhaps is the absence of any coherent factor representing conscientiousness. Rather than being an artefact of measurement or analysis (Weiss et al., 2006), this de-emphasis of conscientiousness is seen as a result of the reduced need in orangutan social structure for the maintenance of such a trait. Orangutans live a semisolitary lifestyle, generally maintaining relatively little contact with other individuals for any significant length of time, excepting the rearing of offspring (Galdikas, 1985b, 1985c). This suggests that either the socially relevant conscientiousness traits have been absorbed into the other factors due to their reduced importance or that these aspects emerged as fully-fledged domain later on in the evolutionary tree (see Chapter 1). This is supported by other reviews suggesting that conscientiousness is more the exception than the rule in a wide range of species (S. D. Gosling & John, 1999; Weiss, 2018).

Gorillas

Only very recently has personality structure been identified in lowland gorillas. Yvonne Baur (unpublished data) has collected personality data on captive gorillas and analysis of this has revealed a six-factor structure. The factor named sociability shares several items with chimpanzee and human extraversion but does not contain the physical aspects of these factors such as Active or Lazy. There are also close similarities between this factor and agreeableness as defined in orangutans and bonobos. The second factor, Dominance, is similar to conscientiousness in bonobos and to dominance in chimpanzees and orangutans but also incorporates some of the negative aspects of conscientiousness in the

latter species. Several of the negative aspects of chimpanzee dominance and neuroticism combine together to make up the emotionality domain in gorillas, though this factor is measured in the inverse to the former two domains. It also incorporates several items representative of assertiveness in bonobos. Negative affect represents several negative aspects of extraversion, agreeableness, assertiveness, and conscientiousness as seen in the other apes as well as the remaining parts of orangutan and chimpanzee neuroticism. Openness in gorillas combines the physical aspects of chimpanzee extraversion with the items associated with openness in both bonobos and chimpanzees. It also closely resembles the extraversion domain as it is defined in orangutans. The last factor, conscientiousness, is quite similar to the eponymous factor in chimpanzees and to the factors of intellect in orangutans and attentiveness in bonobos but with the addition of a few items associated with chimpanzee agreeableness and from the positive aspects of chimpanzee and orangutan dominance.

There is also data on a group of wild mountain gorillas which reveals a different factor structure in this group. Personality in these wild gorillas consists of only four factors (Eckardt et al., 2015). The gorilla factor of dominance is more similar to dominance as defined in chimpanzees (King & Figueredo, 1997) than that seen in orangutans (Weiss et al., 2006), though lacking aspects of "aggressiveness" and including supportive items from chimpanzee agreeableness. Openness in gorillas is more limited in scope than the domains in humans (Goldberg, 1990) and chimpanzees, finding greater similarity to openness in brown capuchins (Morton et al., 2013) and in macaques (Weiss, Adams, Widdig, & Gerald, 2011) due to the inclusion of activity-related items associated with extraversion in other species. Sociability in gorillas appears to be a combinations of elements of agreeableness and extraversion in humans and

chimpanzees, possibly the lack of emphasis on these two traits individually is a result of the stability of gorilla communities compared to the fission-fusion societies observed in other apes (Aureli et al., 2008). The final factor, labelled proto-agreeableness, is more unusual and seems to incorporate traits from low human agreeableness and high orangutan dominance (Eckardt et al., 2015). Along with the lack of a conscientiousness factor, it is notable that there is no independent trait representing neuroticism identified in gorillas.

Naming of Constructs

Looking at the variety of named constructs and hierarchical levels in personality structures across species, it is important to keep in mind the potential problems of the labels we apply. Factor analysis reduces the number of variables into useful factors that summarise the intercorrelations amongst them (Goldberg & Digman, 1994). It is largely for the benefit of the readers' understanding that they are assigned labels attempting to summarise the group of items contained by these higher domains. Issues arise when the semantic meanings of these labels are taken beyond their context and assumptions are made about relationships with other variables. For example, N4: Depression (Costa & McCrae, 1995a) does not contain all of the implications and associations of depression when used in a literary sense nor does it necessarily relate to other psychological topics like major depressive disorder (American Psychiatric Association, 2013). In the context of these factors, we must keep in mind that the whole is in fact *not* greater than the sum of its parts lest we fall into the trap of semantic attribution.

3.1.4 Nuance Analysis in Nonhuman Apes

Since it has been established that personality traits and factor structure in nonhuman apes exist and share key properties of its factor-analytic methods with human five-factor personality, it follows that this structure may too be hierarchical. Indeed, it is possible to reveal an intermediate facet level of organisation using sequential factor analysis (Goldberg, 2006, and see Chapter 2). Building on this idea, we propose that there may also exist a useful item or nuance-level order to nonhuman personality structures. In the present study we look at personality change with age in the great apes (excluding humans). It has been shown that personality at a factor level does correlate with age in humans, chimpanzees, and orangutans (King et al., 2008; Weiss & King, 2015). Interestingly, there are cross-species similarities and some differences in the direction of change (see King et al., 2008). Extraversion and Neuroticism, for example, decrease with age in all three species while Agreeableness increases in humans and chimpanzees but decreases in orangutans (Weiss & King, 2015).

Here we look at this change with age at a nuance level. The purpose of this is to provide a greater degree of specificity in identifying the sources of these age-related changes and to demonstrate the utility in nuance-level analysis as a predictive tool in nonhuman as well as human animals.

In our previous investigation into the facet-level structure of traits (see Chapter 2), we found that many of the facets identified in the personality domains of nonhuman great apes could be defined by only one item. It follows then that there is a possibility that these individual items may be more appropriate and useful than the facet level we have identified. These two studies represent the majority of the work on nonhuman personality facets other than their a priori definition borrowed from human facets (King & Weiss, 2011; King

et al., 2008; Weiss & King, 2015). Overall, looking at lower-orders in personality can provide us with more detail and a more differentiated perspective of the measurement of traits with greater specificity (Paunonen et al., 1992; Briggs, 1989; A. H. Buss, 1989; Mershon & Gorsuch, 1988). While these arguments were originally used to support the use of facet-level structure (Costa & McCrae, 1995a), the same arguments hold true for nuances (McCrae, 2015; Mõttus et al., 2017). Specifically, what we can hope to get out of personality at this scale is a model that maximises the accounting for item-specific variance, which contributes to retest reliability, a better predictor of validity than internal consistency (McCrae, 2015). These item level analyses can provide a more comprehensive description of personality and can be used to predict outcomes in conceptually meaningful ways (Mõttus et al., 2017, 2018). As a metric of this, we wanted to use a standard that was widely applicable to all species involved with a history of research and clearly defined at the domain level (King et al., 2008; Weiss & King, 2015). Personality development with age fit this description very well with the added advantage of being determined from readily available data (for a review see Chapter 1). The advantage of comparing data from multiple species is that we can use these analyses to infer how the differences in these relationships evolved by looking at the evolutionary tree of hominids and applying what S. D. Gosling and Graybeal (2007) refers to as tree-thinking. Through this we can greatly increase our understanding of both the practical concerns of predicting outcomes with personality and the broader evolutionary understanding of personality in primates.

3.2 Methods

3.2.1 Subjects

Chimpanzees

Subjects consisted of 533 captive chimpanzees (324 female, mean age = 16.52 years) of which 156 had full HPQ ratings while the remaining 378 had only the CPQ items. These samples were first described elsewhere (King & Figueredo, 1997; King et al., 2008; Weiss et al., 2007, 2009, 2012). Collected as a part of the original investigation into the chimpanzee factor model and CPQ, the first group consists of 100 chimpanzees (59 female, mean age = 18.4 years) comes from King and Figueredo (1997). Personality data were collected on chimpanzees from 12 zoos in the United States participating in the Chimpan-Zoo program run by the Jane Goodall Institute. Expanding the Chimpan-zoo dataset, 102 chimpanzees from five other participating zoos in the United States and one in Australia (King et al., 2008). All together, this first combined dataset contained personality data from 78 male and 124 female chimpanzees with an average age of 16.5 years. A separately organised dataset was collected from the Yerkes National Primate Research Center in the United States by Weiss et al. (2007) and then added to the total pool. In that study, data were collected on 175 new captive chimpanzees (107 female, mean age = 20.5) housed at Yerkes in Atlanta, Georgia, USA.

The growing dataset was further expanded both in number of individuals and number of items by utilising the HPQ to collect data on 146 chimpanzees (86 female, mean age = 22.0 years) from seven zoos and two research institutes in Japan (Weiss et al., 2009). In a later study, an additional four males and

six females from two more Japanese zoos (Weiss et al., 2012) were added.

Bonobos

The bonobo subjects, collected by Weiss et al. (2015) to describe the bonobo personality structure, constitute around 80% of the total captive bonobo population in the United States and Europe. Data were collected from five zoos in Germany and one each in Belgium, the Netherlands, and the United Kingdom as well as seven zoos and one research institute in the United States. In total, personality data on 154 bonobos (83 female, mean age = 16.2 years) is included in the sample.

Orangutans

Beginning with the 152 orangutan subjects used to originally determine the factor structure of orangutan personality and later increasing to 174 (104 female, mean age = 21.7 years), this dataset consists of captive individuals from groups described in two previous studies (Weiss et al., 2006, 2012). These orangutans were housed in 38 zoos in the United States, two in Canada, one in Australia, and one in Singapore.

Gorillas

Data on captive western lowland gorillas comes from individuals housed in 30 zoos in the United States, Canada, the Netherlands, and Japan. In total there are 203 gorillas (115 female, mean age = 20.3). This dataset was used to determine the factor structure of captive individuals of the species.

3.2.2 Raters and Ratings

Ratings of all species were conducted by individuals familiar with the animals largely consisting of researchers, caretakers, and volunteers at the various facilities. These raters were able to reliably score the animals they were tasked to assess. The mean length of time they had experience with the individual animals was between five and six years for all datasets. In most cases, the minimum familiarity time for these raters would be at least one year, however this was not always the case for practical reasons. The data provided by these raters was still reliable and accurate in comparison with raters who were at their respective facilities for greater lengths of time. Each individual animal also received ratings from between one and eight raters, again ideally more than one rater would be used and the average scores would be taken but in a few instances practical considerations did not allow this.

In their instructions, raters were told to give an overall impression of the individual's behaviour for their ratings rather than specific frequency data or anecdotal examples.

3.2.3 Questionnaires

Data were collected from all species using three personality measures, the Chimpanzee Personality Questionnaire (CPQ, King & Figueredo, 1997), the Orangutan Personality Questionnaire (OPQ, Weiss et al., 2006), and the Hominoid Personality Questionnaire (HPQ, King et al., 2006). These three measures represent an evolution of the instruments to become more widely applicable and to better represent personality dimensions in the species, with each scale containing progressively more items. These data were collected over a long

period of time and represent a large portion of all personality data collected on great apes using this family of questionnaires. We included all of these data in the present study to make use of the greatest available quantity of data and resources. In particular, the overlap between the CPQ and HPQ means that some integration of data is possible between the two chimpanzee groups and the most data are utilised.

The CPQ consists of 43 personality related descriptive adjectives that are incorporated into complete statements. These statements consist of one to three sentences and are used to put the descriptor adjectives in the context of primate behaviour. This questionnaire was developed by King and Figueredo (1997) and consists of 41 adjectives derived from the human Big Five (Goldberg, 1990) and two that were added specifically for rating chimpanzees.

The OPQ adds five items to the 43 present in the CPQ (Weiss et al., 2006) to make a questionnaire more appropriate to measuring personality in orangutans. The primary reason for the addition of these new items was to address issues with the representation of the neuroticism and openness domains in orangutans as they were originally identified in chimpanzees (King et al., 2005). Later, the HPQ adds to the original CPQ these five items representing openness and neuroticism (Weiss et al., 2006) and six representing openness and conscientiousness (Weiss et al., 2009).

In all measures items are given a rating on a scale from one ("displays total absence or negligible amounts of the trait") to seven ("displays extremely large amounts of the trait"). Interrater reliabilities, internal consistencies, and test-retest reliabilities are consistently high in studies using these measures.

The questionnaires were originally developed in English, though raters from

non-English speaking countries used versions translated to their native language and validated so as to allow them to more accurately represent their interpretations.

3.2.4 Analyses

Nuance-Age Correlation

In this study, the goal was to investigate the relationship between age and personality in a cross-sectional personality dataset. To that end, we correlated each personality item individually with age to compare with the overall factor scores and their age correlations.

3.3 Results

3.3.1 Chimpanzees

CPQ

At the factor level, we found that only three of the six domains in chimpanzee personality, extraversion ($t=-17.28$, $p<0.001$, $r=-.60$), openness ($t=-8.95$, $p<0.001$, $r=-.36$), and dominance ($t=3.80$, $p<0.001$, $r=.16$) were significantly associated with age. The remaining three, conscientiousness ($t=1.81$, $p=0.07$, $r=.08$), neuroticism ($t=1.68$, $p=0.09$, $r=.07$), and agreeableness ($t=1.40$, $p=0.16$, $r=.06$) were not.

Extraversion All items in extraversion showed significant correlations with age of varying strengths though all were negative.

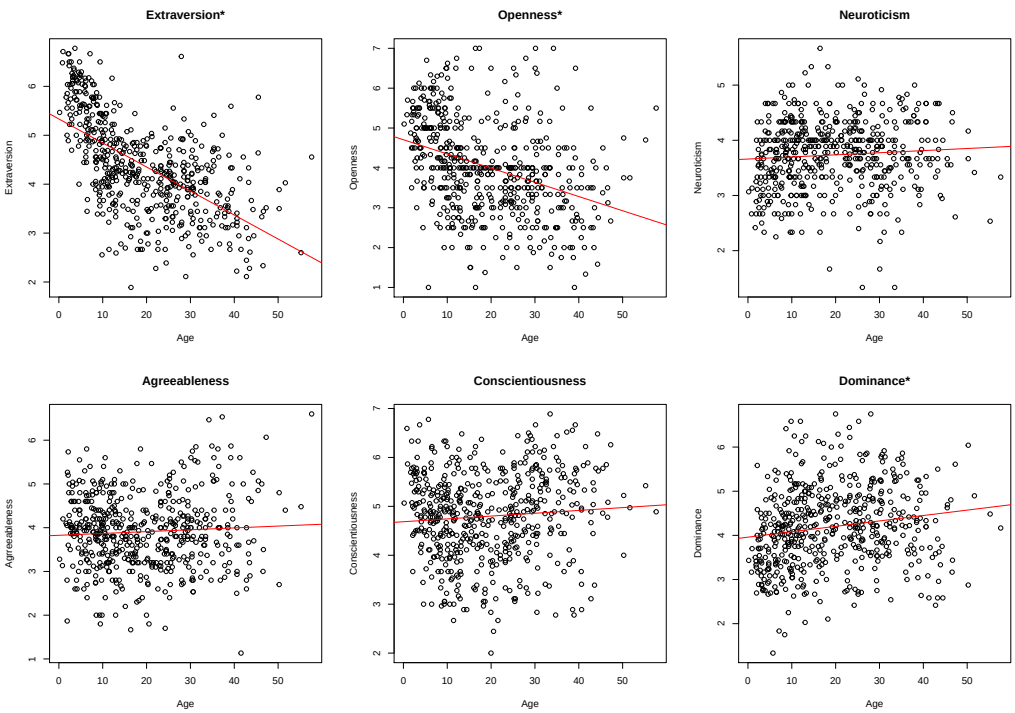

Figure 3.1: Correlations between age and factor score in chimpanzees using the CPQ.

Table 3.1: Correlations between CPQ Extraversion and Age

Item	t-score	p-value	r
Active	-21.60	<0.001*	-.68
Playful	-19.81	<0.001*	-.65
Sociable	-9.11	<0.001*	-.37
Friendly	-5.75	<0.001*	-.24
Affectionate	-4.68	<0.001*	-.20
Imitative	-12.18	<0.001*	-.47
Solitary(-)	-10.81	<0.001*	-.42
Lazy(-)	-17.34	<0.001*	-.60
Depressed(-)	-5.67	<0.001*	-.24

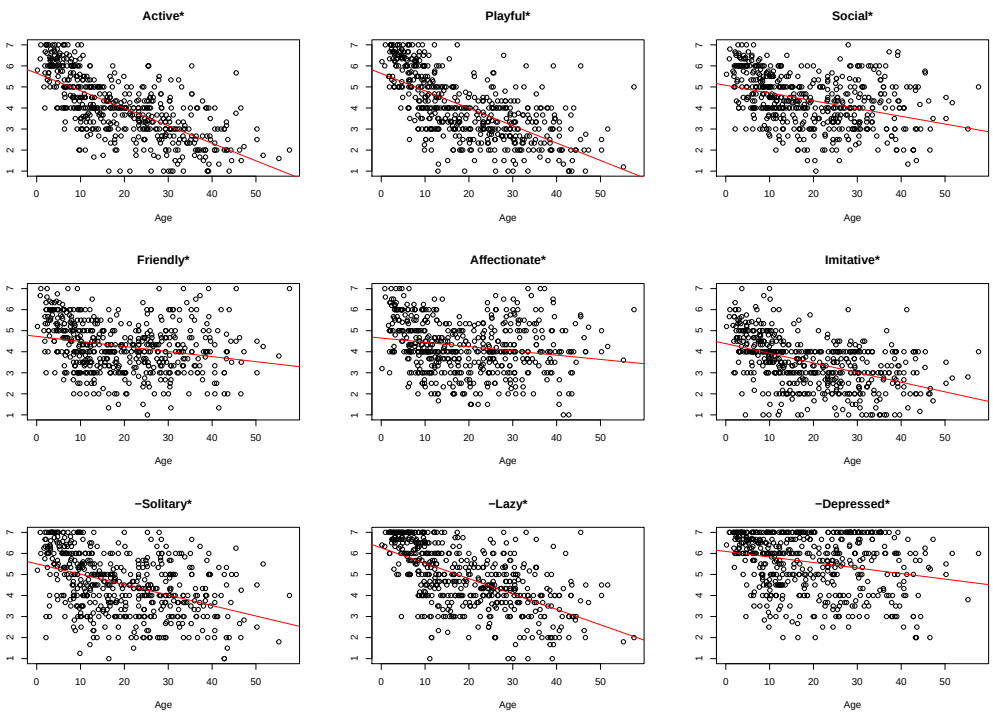

Figure 3.2: Correlations between age and extraversion items in chimpanzees using the CPQ.

Table 3.2: Correlations between CPQ Conscientiousness and Age

Item	t-score	p-value	r
Predictable	5.21	<0.001*	.22
Impulsive(-)	3.45	<0.001*	.15
Defiant(-)	1.12	0.265	.05
Reckless(-)	4.78	<0.001*	.20
Erratic(-)	0.92	0.357	.04
Irritable(-)	-4.16	<0.001*	-.18
Aggressive(-)	-0.04	0.971	-.00
Jealous(-)	2.06	0.040*	.09
Disorganised(-)	-1.00	0.320	-.04

Table 3.3: Correlations between CPQ Neuroticism and Age

Item	t-score	p-value	r
Excitable	-1.45	0.148	-.06
Stable(-)	-2.27	0.023*	-.10
Unemotional	6.75	<0.001*	.28

Conscientiousness Only Predictable, and the reversed scored Impulsive, Reckless, Irritable, and Jealous showed significant correlations with age. All were weak positive correlations except for Irritable which was weakly negative.

Neuroticism The negatively scored Stable showed a significant negative correlation with age while Unemotional correlated positively. Both were weak correlations and Excitable did not have a significant relationship with age.

Agreeableness Only Protective varied with age showing a weak positive correlation. All other items were non-significant.

Openness Both items in openness showed significant negative correlations with age.

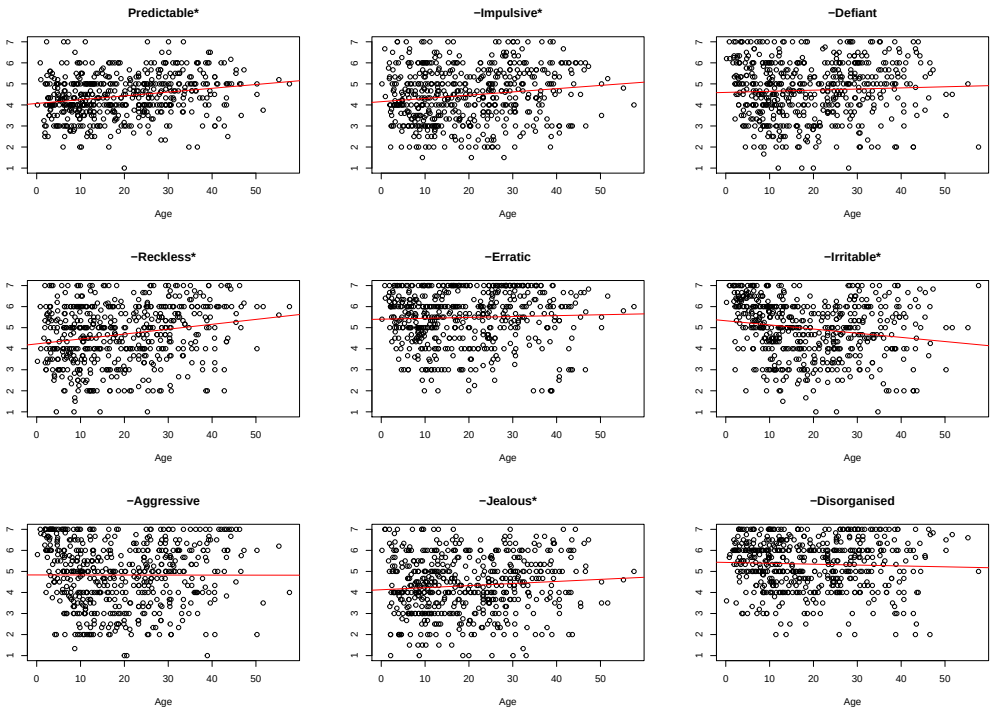

Figure 3.3: Correlations between age and conscientiousness items in chimpanzees using the CPQ.

Table 3.4: Correlations between CPQ Agreeableness and Age

Item	t-score	p-value	r
Sympathetic	1.57	0.117	.07
Helpful	-0.87	0.383	-.03
Sensitive	0.51	0.608	.02
Protective	3.55	<0.001*	.15
Gentle	0.55	0.584	.02

Table 3.5: Correlations between CPQ Openness and Age

Item	t-score	p-value	r
Inquisitive	-9.88	<0.001*	-.39
Inventive	-6.79	<0.001*	-.28

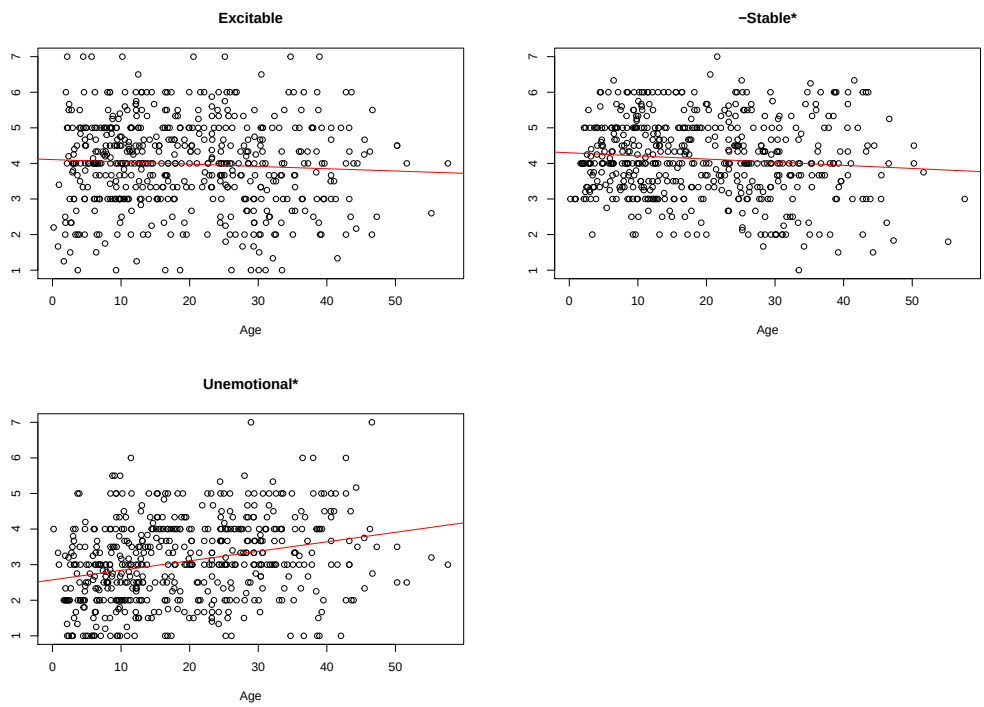

Figure 3.4: Correlations between age and neuroticism items in chimpanzees using the CPQ.

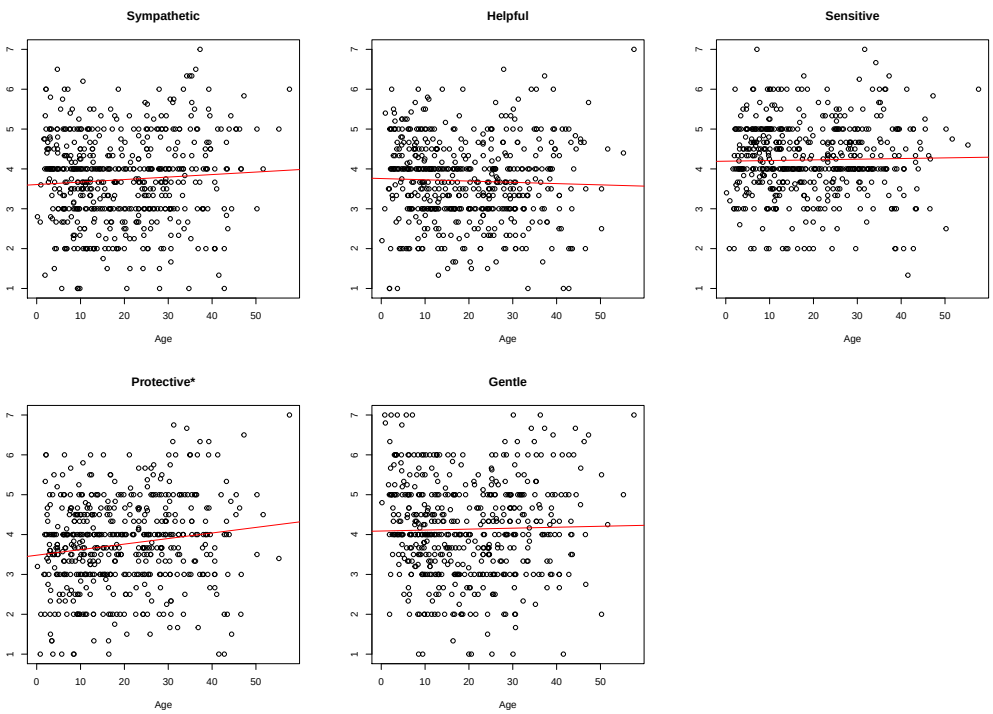

Figure 3.5: Correlations between age and agreeableness items in chimpanzees using the CPQ.

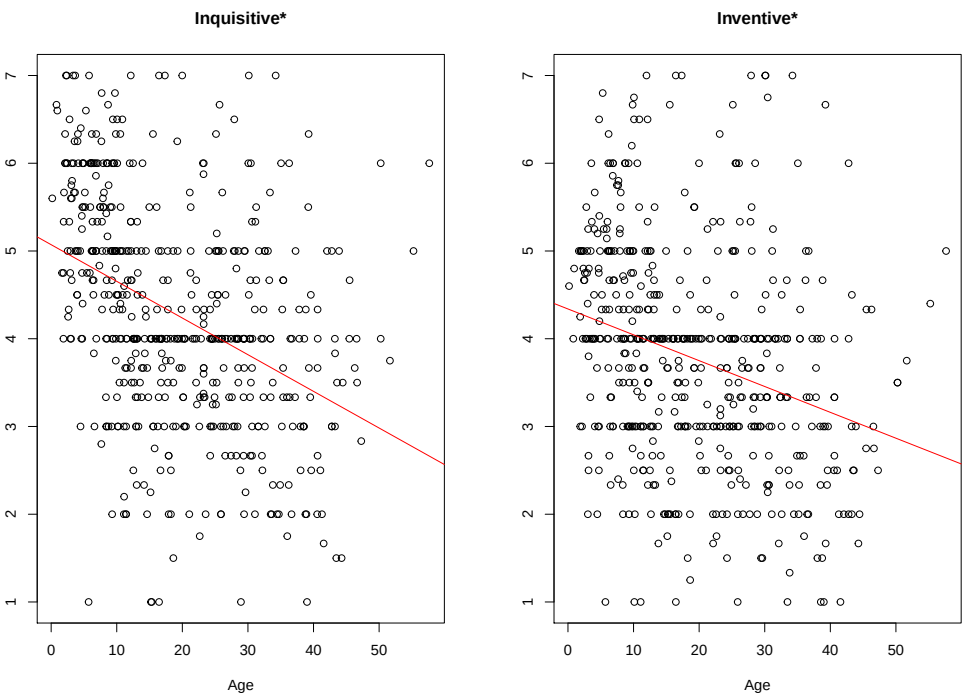

Figure 3.6: Correlations between age and openness items in chimpanzees using the CPQ.

Table 3.6: Correlations between CPQ Dominance and Age

Item	t-score	p-value	r
Dominant	5.01	<0.001*	.21
Independent	5.85	<0.001*	.25
Decisive	2.76	0.005*	.11
Intelligent	0.10	0.919	.00
Persistent	-1.41	0.159	-.06
Bullying	0.27	0.789	.01
Stingy	2.52	0.012*	-.11
Submissive(-)	3.74	<0.001*	.16
Dependent(-)	7.68	<0.001*	.32
Fearful(-)	3.80	<0.001*	.16
Timid(-)	0.13	0.900	.01
Cautious(-)	-0.14	0.889	-.01

Dominance Dominant, Independent, Decisive, Stingy, Submissive, Dependent, and Fearful all correlated significantly with age. All were positive except for Stingy.

HPQ

In the full HPQ factor level the same three factors, extraversion (t=-6.84, p<0.001, r=-.48), openness (t=-5.62, p<0.001, r=-.41), and dominance (t=2.52, p=0.012, r=.20) correlated significantly with age. Conscientiousness (t=1.34, p=0.18, r=.11), neuroticism (t=-1.10, p=0.27, r=-.09), and agreeableness (t=1.71, p=0.09, r=.14) did not significantly vary with age.

Extraversion Weak to moderate negative correlations were seen between age and the items Active, Playful, Sociable, Imitative, Solitary, and Lazy.

Conscientiousness Here the only significant variation with age was seen in Predictable, Thoughtless, and Distractible which was all positive and weak to

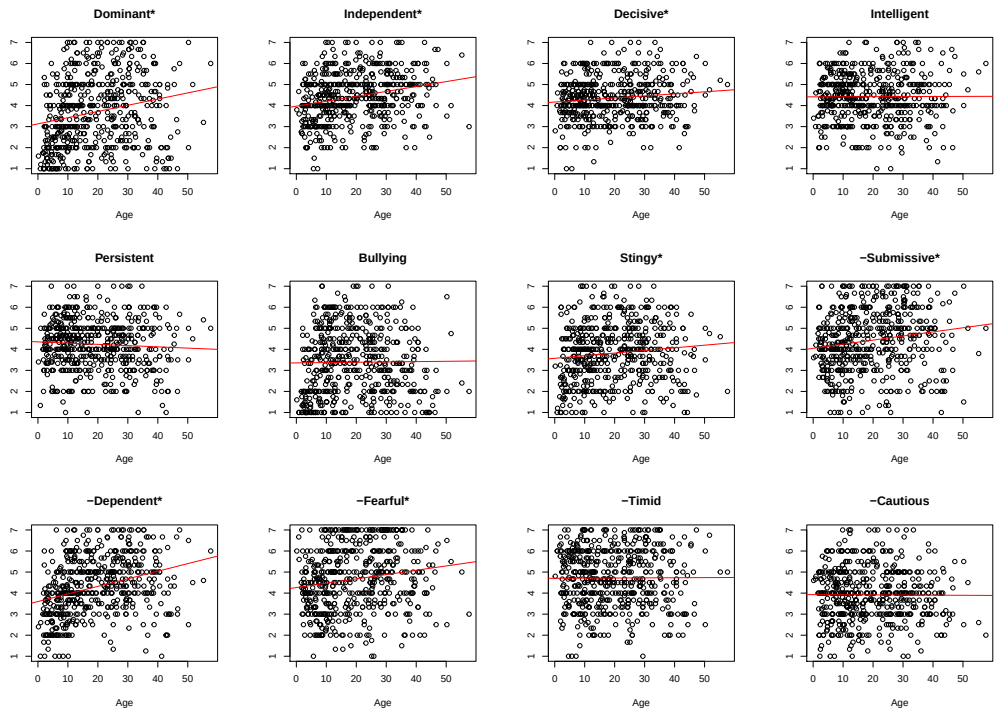

Figure 3.7: Correlations between age and dominance items in chimpanzees using the CPQ.

Table 3.7: Correlations between HPQ Extraversion and Age

Item	t-score	p-value	r
Active	-8.81	<0.001*	-.58
Playful	-8.74	<0.001*	-.55
Sociable	-2.91	0.004*	-.23
Friendly	-0.68	0.499	-.05
Affectionate	-0.44	0.661	-.04
Imitative	-6.26	<0.001*	-.45
Solitary(-)	-3.18	0.002*	-.25
Lazy(-)	-7.00	<0.001*	-.49
Depressed(-)	-0.86	0.391	-.07
Individualistic	-1.85	0.066	-.15

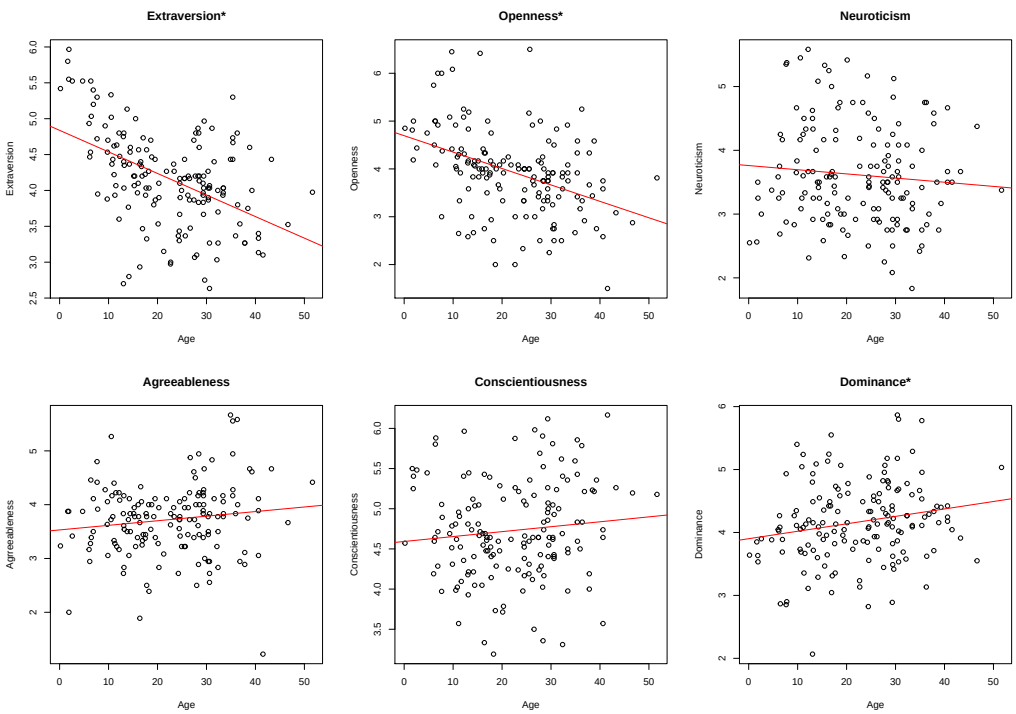

Figure 3.8: Correlations between age and factor score in chimpanzees using the HPQ.

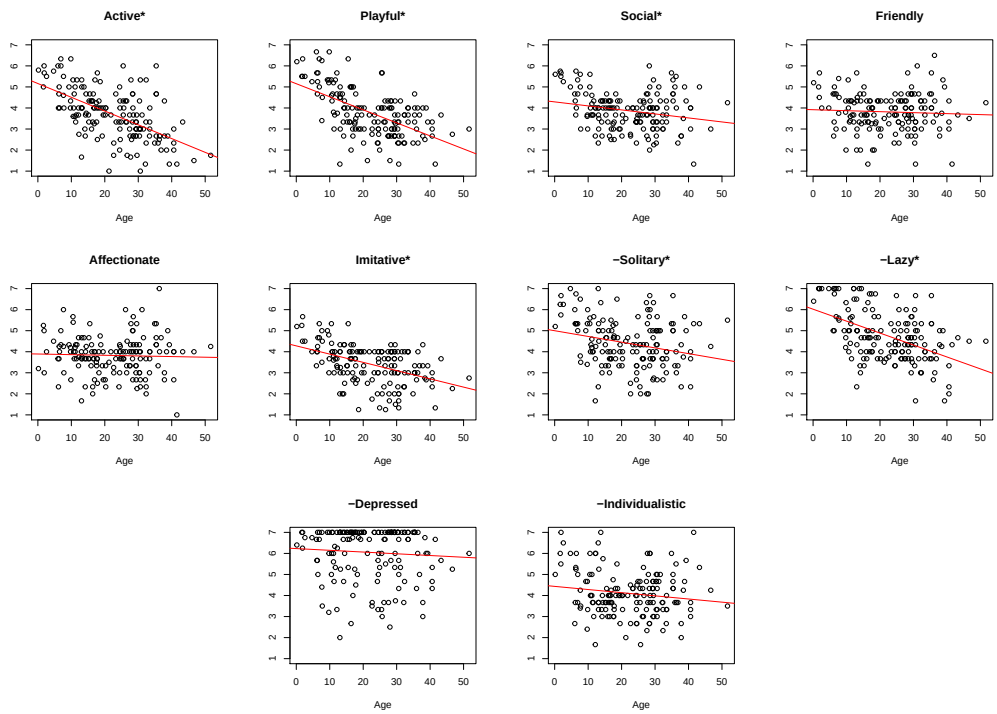

Figure 3.9: Correlations between age and extraversion items in chimpanzees using the HPQ.

Table 3.8: Correlations between HPQ Conscientiousness and Age

Item	t-score	p-value	r
Predictable	5.32	<0.001*	.39
Impulsive(-)	0.34	0.735	-.05
Defiant(-)	-0.61	0.544	.05
Reckless(-)	1.33	0.186	.11
Erratic(-)	1.12	0.263	.09
Irritable(-)	0.13	0.896	.01
Aggressive(-)	0.03	0.975	-.00
Jealous(-)	0.44	0.664	.03
Disorganised(-)	1.42	0.159	.11
Clumsy(-)	-0.95	0.343	-.08
Thoughtless(-)	4.05	<0.001*	.31
Distractible(-)	2.38	0.019*	.19
Unperceptive(-)	-1.12	0.264	-.09
Quitting(-)	-1.27	0.207	-.10

Table 3.9: Correlations between HPQ Neuroticism and Age

Item	t-score	p-value	r
Excitable	1.28	0.203	.01
Autistic	-0.79	0.431	-.06
Stable(-)	-1.22	0.224	-.10
Cool(-)	-3.09	0.002*	-.24

moderate.

Neuroticism Cool was the only item to vary with age in neuroticism, showing a weak negative correlation.

Agreeableness All items did not show significant variation with age except for Conventional which had a weak positive association.

Openness All items in openness showed a moderate negative correlation with age.

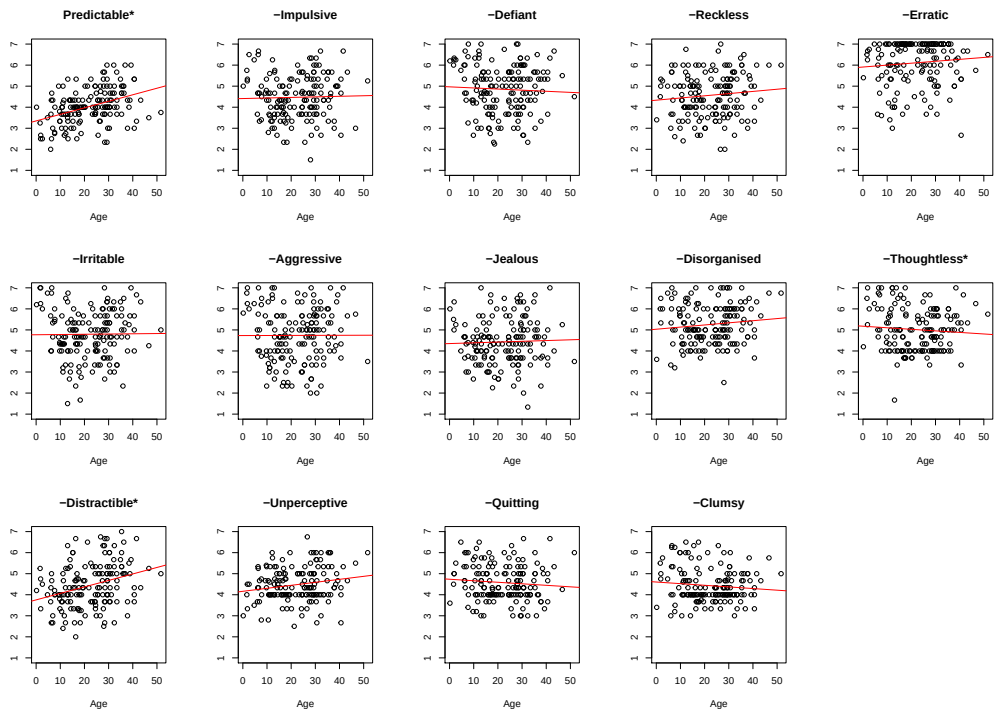

Figure 3.10: Correlations between age and conscientiousness items in chimpanzees using the HPQ.

Table 3.10: Correlations between HPQ Agreeableness and Age

Item	t-score	p-value	r
Sympathetic	0.57	0.568	.05
Helpful	1.59	0.115	.13
Sensitive	0.70	0.484	.06
Protective	0.52	0.601	.04
Gentle	1.09	0.276	.09
Conventional	3.78	<0.001*	.29

Table 3.11: Correlations between HPQ Openness and Age

Item	t-score	p-value	r
Inquisitive	-5.27	<0.001*	-.39
Inventive	-5.11	<0.001*	-.38
Curious	-3.94	<0.001*	-.31
Innovative	-5.50	<0.001*	-.40

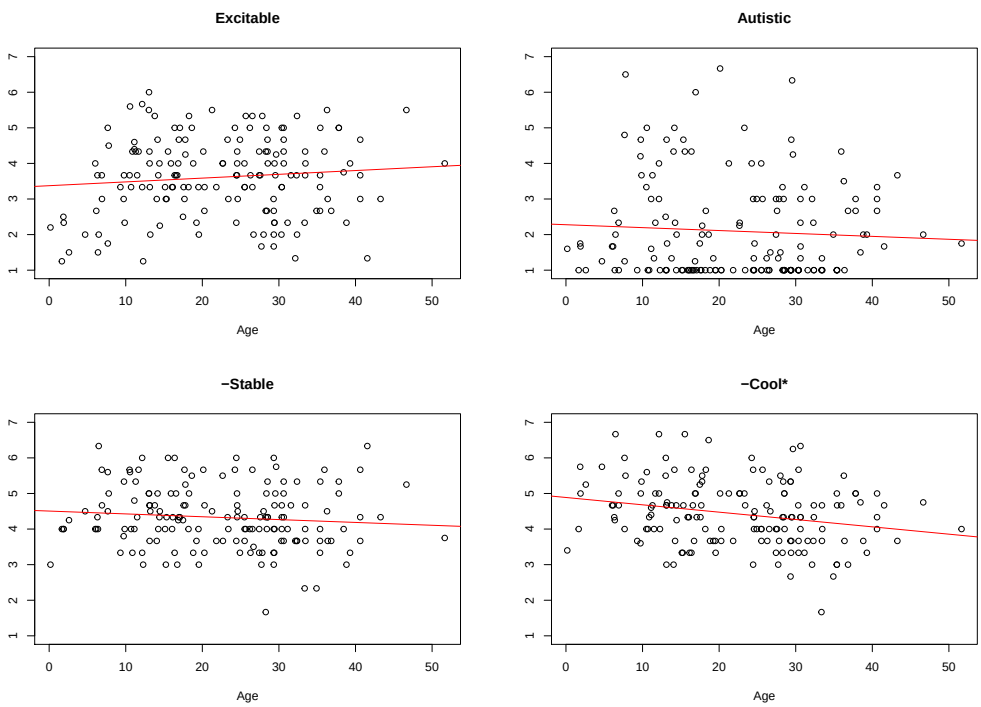

Figure 3.11: Correlations between age and neuroticism items in chimpanzees using the HPQ.

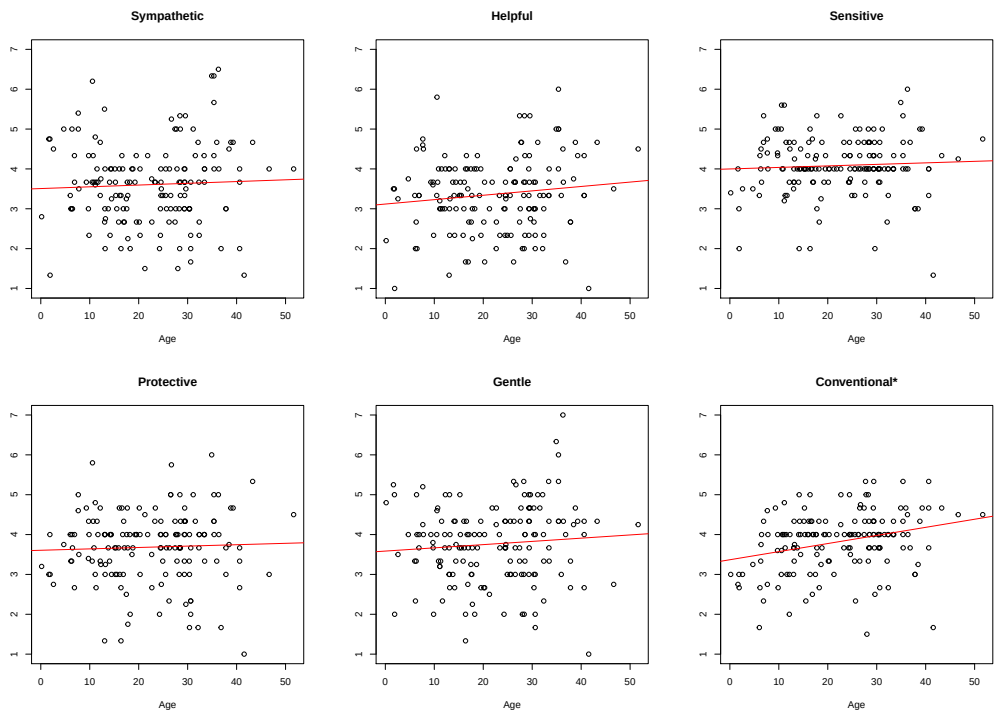

Figure 3.12: Correlations between age and agreeableness items in chimpanzees using the HPQ.

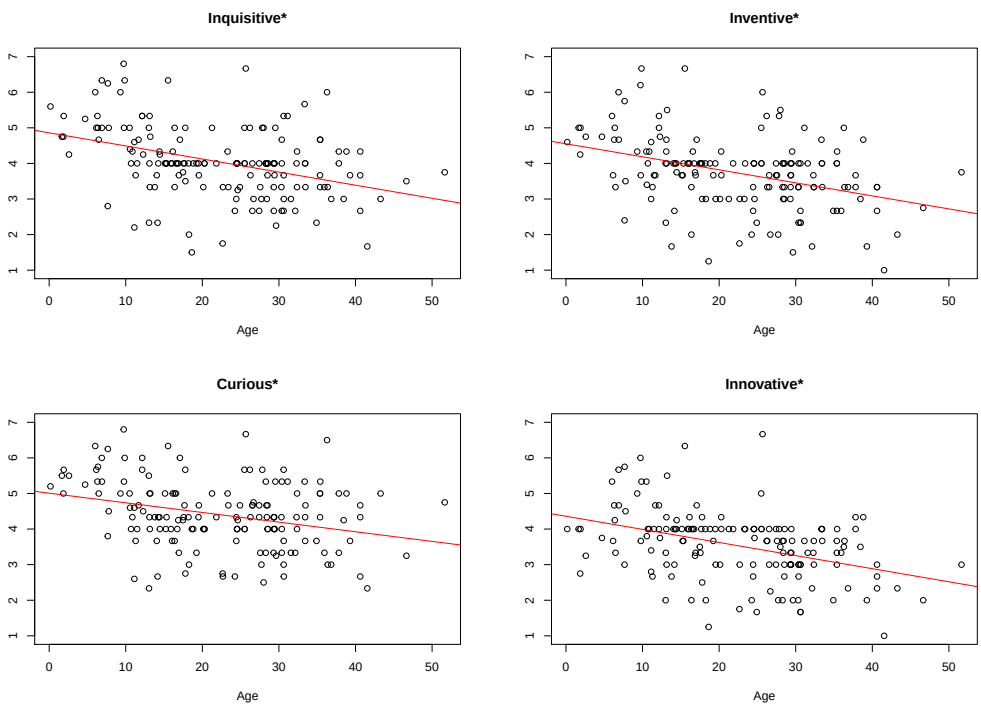

Figure 3.13: Correlations between age and openness items in chimpanzees using the HPQ.

Table 3.12: Correlations between HPQ Dominance and Age

Item	t-score	p-value	r
Dominant	2.26	0.025*	.18
Independent	3.28	0.001*	.26
Decisive	1.12	0.263	.09
Intelligent	-0.51	0.611	-.04
Persistent	-0.88	0.382	-.07
Bullying	0.62	0.536	.05
Stingy	0.70	0.487	.06
Manipulative	1.19	0.235	.10
Submissive(-)	2.42	0.017*	.19
Dependent(-)	4.55	<0.001*	.34
Fearful(-)	2.18	0.031*	.17
Timid(-)	2.03	0.044*	.16
Cautious(-)	1.07	0.285	.09
Vulnerable(-)	0.19	0.850	.02
Anxious(-)	0.23	0.819	.02

Dominance Dominant, Independent, Submissive, Dependent, Fearful, and Timid correlated positively with age. The remaining items did not vary significantly.

3.3.2 Bonobos

In bonobos, three factors varied significantly with age. These were extraversion (t=-2.48, p=0.014, r=-.20), openness (t=-9.08, p<0.001, r=-.41), and agreeableness (t=2.18, p=0.030, r=.17). Correlations with the other three factors, conscientiousness (t=1.12, p=0.264, r=.09), attentiveness (t=0.87, p=0.388, r=-.15), and assertiveness (t=1.91, p=0.059, r=.15) were not significant.

Extraversion Solitary was the only item to vary with age in this factor. It showed a moderate negative correlation.

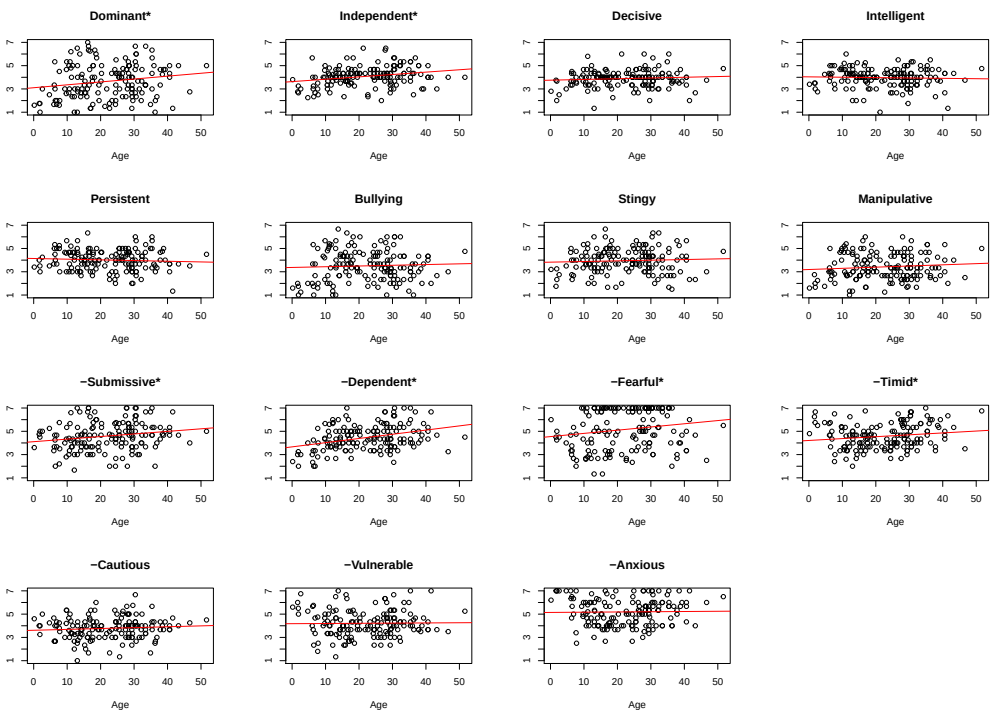

Figure 3.14: Correlations between age and dominance items in chimpanzees using the HPQ.

Table 3.13: Correlations between Bonobo Extraversion and Age

Item	t-score	p-value	r
Solitary(-)	-4.42	<0.001*	-.38
Depressed(-)	-1.91	0.058	-.15
Autistic(-)	-0.68	0.495	-.06
Individualistic(-)	-0.24	0.808	-.02

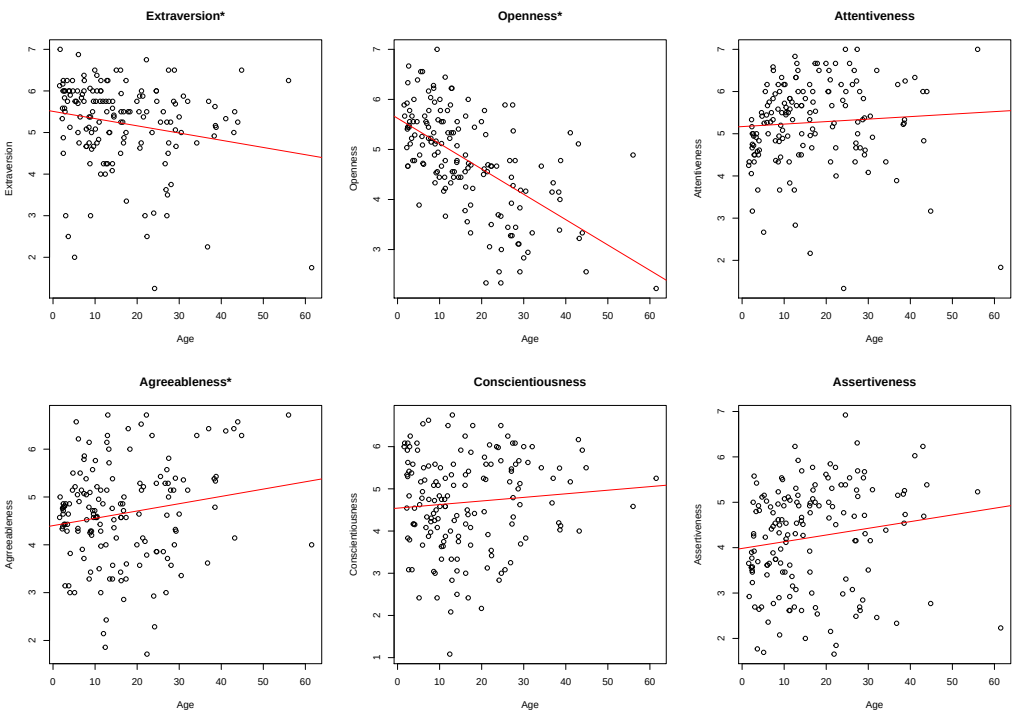

Figure 3.15: Correlations between age and factor scores in bonobos using the HPQ.

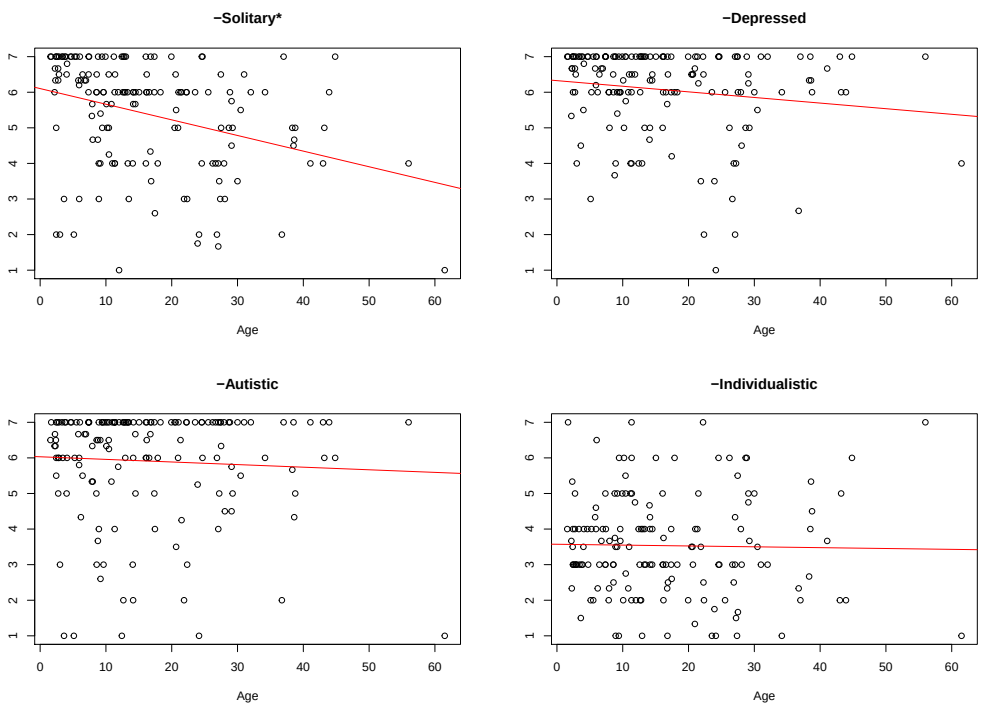

Figure 3.16: Correlations between age and extraversion items in bonobos using the HPQ.

Table 3.14: Correlations between Bonobo Conscientiousness and Age

Item	t-score	p-value	r
Bullying(-)	0.19	0.846	.02
Aggressive(-)	0.28	0.778	.02
Stingy(-)	-0.11	0.911	-.01
Irritable(-)	-2.21	0.028*	-.18
Jealous(-)	1.83	0.069	.15
Gentle	1.87	0.063	.15
Erratic(-)	0.14	0.886	.01
Defiant(-)	1.83	0.069	.15
Reckless(-)	2.12	0.036*	.17
Manipulative(-)	-0.78	0.438	-.06
Predictable	1.85	0.066	.15
Impulsive(-)	3.06	0.003*	.24

Table 3.15: Correlations between Bonobo Attentiveness and Age

Item	t-score	p-value	r
Disorganised(-)	1.33	0.185	.11
Intelligent	0.40	0.687	.03
Clumsy(-)	0.00	0.996	.00
Thoughtless(-)	0.41	0.681	.03
Distractible(-)	3.38	0.001*	.26
Unperceptive(-)	-1.85	0.067	-.15

Conscientiousness Reckless and Impulsive correlated positively with age while Irritable showed a negative association. All correlations were weak in magnitude.

Attentiveness Only Distractible showed significant variation, correlating positively with age.

Agreeableness Protective and Sensitive both showed moderate positive correlations with age within the agreeableness factor.

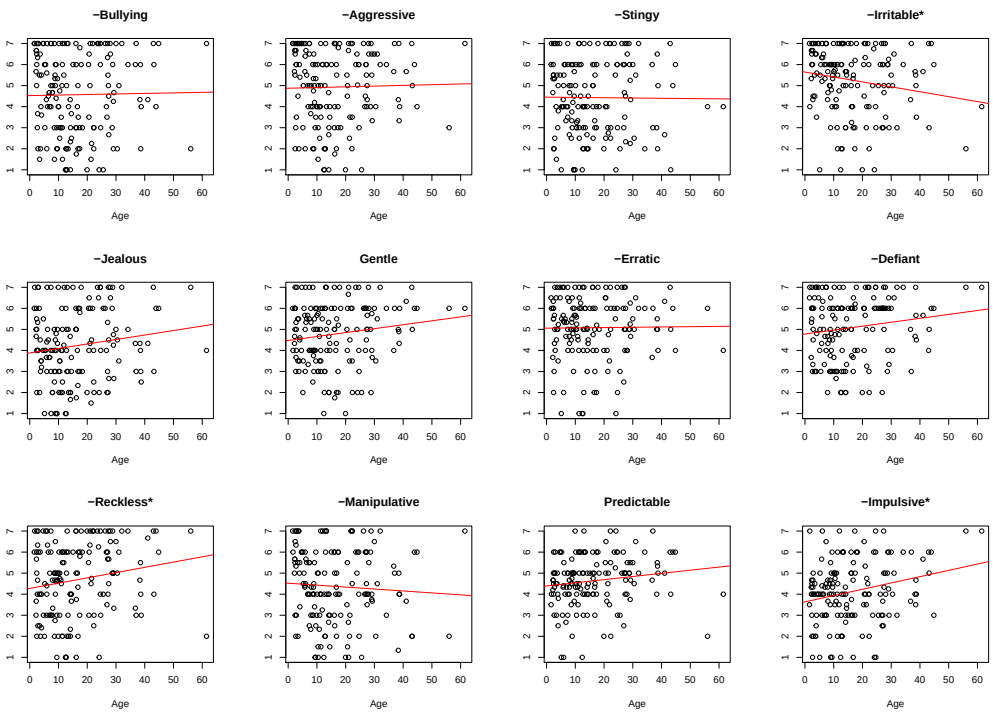

Figure 3.17: Correlations between age and conscientiousness items in bonobos using the HPQ.

Table 3.16: Correlations between Bonobo Agreeableness and Age

Item	t-score	p-value	r
Friendly	-1.15	0.253	-.09
Affectionate	0.18	0.856	.01
Protective	4.85	<0.001*	.37
Sympathetic	3.37	0.001*	.26
Helpful	1.08	0.283	.09
Sociable	-1.31	0.191	-.11
Sensitive	3.91	<0.001*	.30

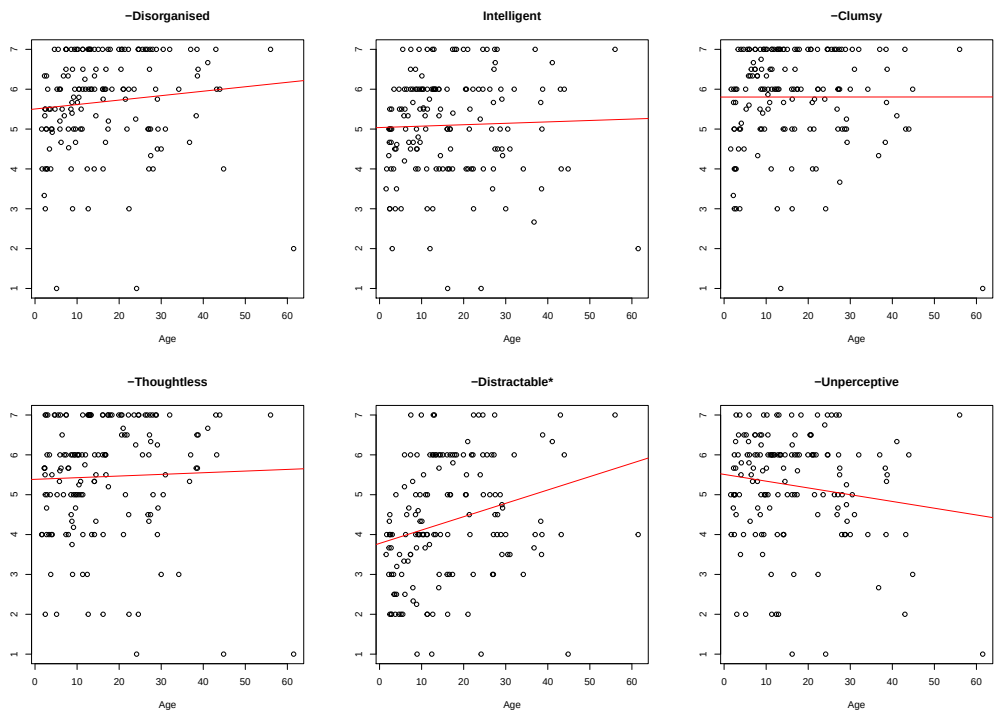

Figure 3.18: Correlations between age and attentiveness items in bonobos using the HPQ.

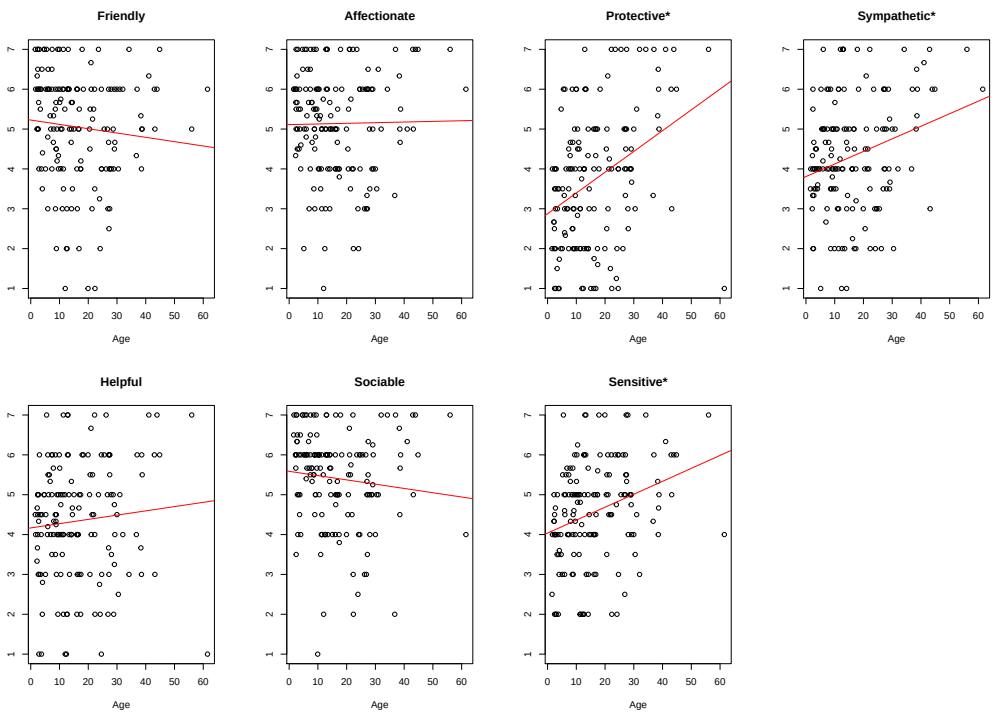

Figure 3.19: Correlations between age and agreeableness items in bonobos using the HPQ.

Table 3.17: Correlations between Bonobo Openness and Age

Item	t-score	p-value	r
Active	-13.14	<0.001*	-.73
Playful	-7.50	<0.001*	-.52
Inquisitive	-5.20	<0.001*	-.39
Inventive	-2.45	0.016*	-.19
Imitative	-7.99	<0.001*	-.54
Innovative	-3.36	<0.001*	-.26
Conventional(-)	-4.60	<0.001*	-.35
Curious	-3.55	<0.001*	-.28
Lazy(-)	-5.58	<0.001*	-.41

Openness All items in openness showed significant negative correlations with age ranging in magnitude from weak to strong.

Assertiveness Dominant, Submissive, and Dependent were the only items to vary with age and show weak to moderate positive associations.

3.3.3 Orangutans

In orangutans, the factors of extraversion (t=-11.98, p<0.001, r=-.67), neuroticism (t=-4.13, p<0.001, r=-.30), agreeableness (t=-3.30, p=0.001, r=-.24), and intellect (t=6.08, p<0.001, r=.42) all showed significant correlations with age while only dominance (t=1.38, p=0.169, r=.10) showed no relationship with age.

Extraversion All items in extraversion correlate negatively with age to a moderate or high degree.

Dominance The items Dominant, Submissive, and Irritable vary positively with age while Manipulative and Reckless show a negative association.

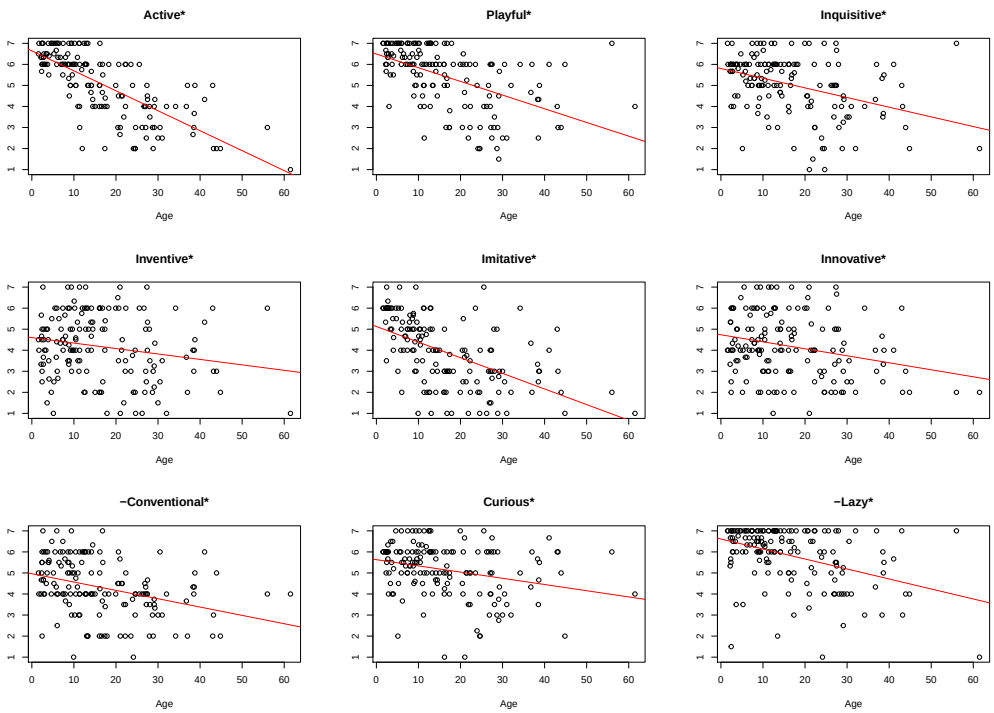

Figure 3.20: Correlations between age and openness items in bonobos using the HPQ.

Table 3.18: Correlations between Bonobo Assertiveness and Age

Item	t-score	p-value	r
Anxious(-)	-0.12	0.905	-.01
Timid(-)	1.03	0.306	.08
Fearful(-)	0.15	0.880	.01
Independent	2.30	0.023*	.18
Dominant	4.25	<0.001*	.33
Vulnerable(-)	0.76	0.449	.06
Submissive(-)	2.25	0.026*	.18
Cool	1.45	0.148	.12
Stable	-0.29	0.774	-.02
Dependent(-)	3.90	<0.001*	.30
Decisive	1.40	0.163	.11
Persistent	0.71	0.481	.06
Excitable	-1.03	0.302	-.08

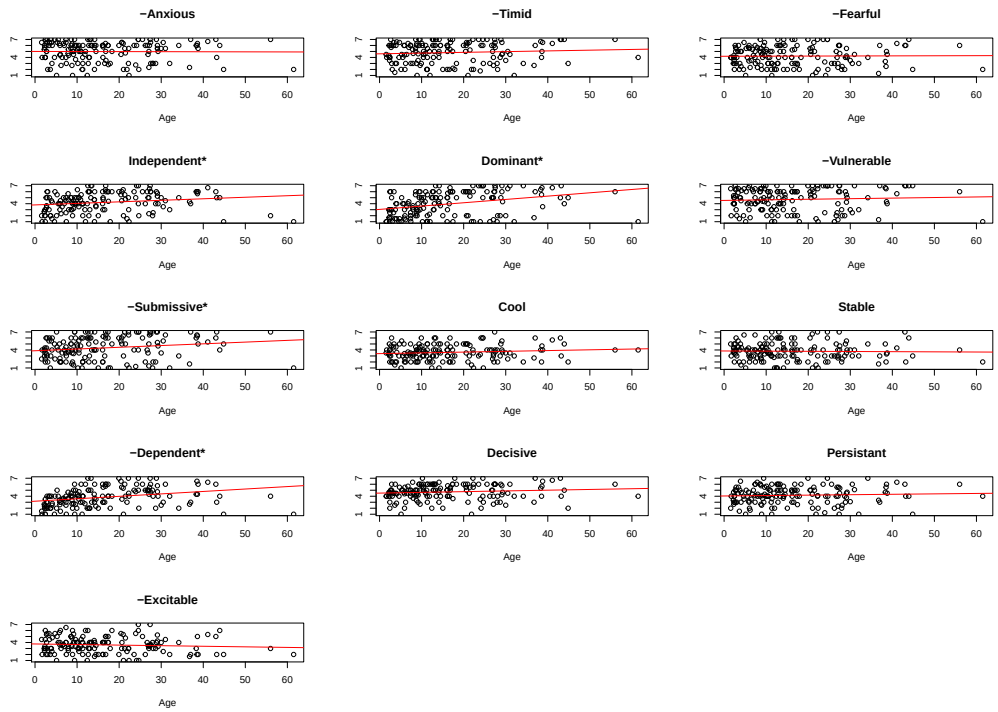

Figure 3.21: Correlations between age and assertiveness items in bonobos using the HPQ.

Table 3.19: Correlations between Orangutan Extraversion and Age

Item	t-score	p-value	r
Playful	-12.64	<0.001*	-.69
Active	-11.05	<0.001*	-.64
Lazy(-)	-10.25	<0.001*	-.62
Curious	-6.41	<0.001*	-.44
Conventional(-)	-5.63	<0.001*	-.39
Inquisitive	-4.93	<0.001*	-.35
Inventive	-4.46	<0.001*	-.32
Solitary(-)	-7.99	<0.001*	-.52
Unemotional(-)	-4.73	<0.001*	-.34
Imitative	-9.66	<0.001*	-.59
Depressed(-)	-4.84	<0.001*	-.35

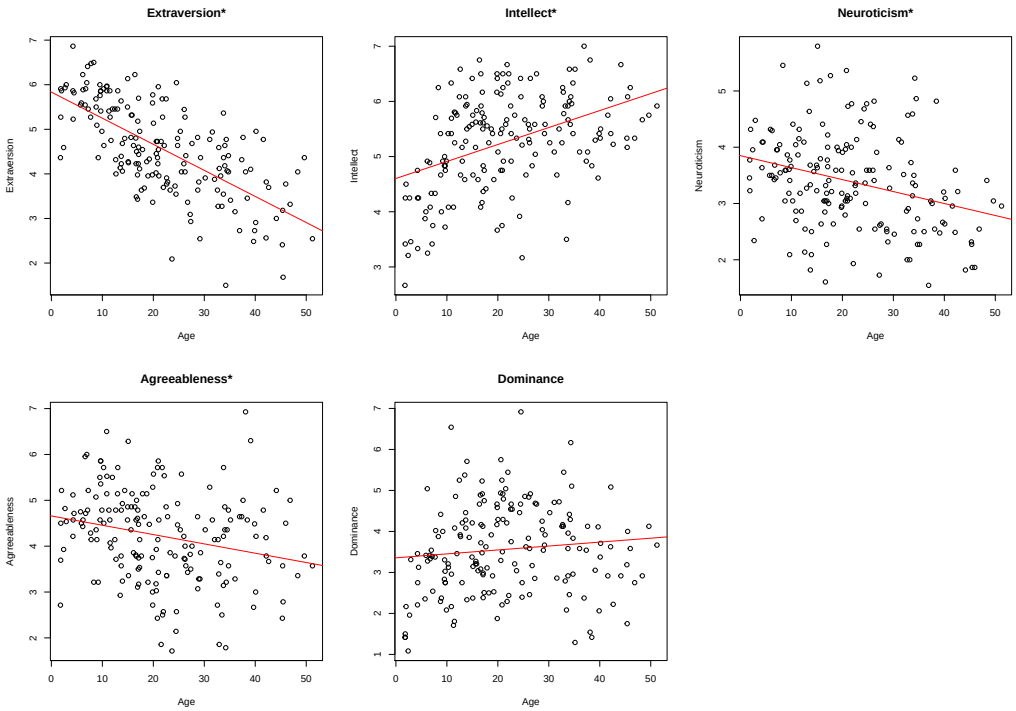

Figure 3.22: Correlations between age and factor scores in orangutans using the OPQ.

Table 3.20: Correlations between Orangutan Dominance and Age

Item	t-score	p-value	r
Bullying	1.61	0.110	.12
Aggressive	2.02	0.045*	.15
Stingy	0.10	0.923	.01
Jealous	-0.44	0.658	-.03
Dominant	4.65	<0.001*	.33
Gentle(-)	0.63	0.527	.05
Defensive	-0.03	0.980	-.00
Submissive(-)	3.92	<0.001*	.29
Manipulative	-2.03	0.044*	-.15
Persistent	0.21	0.832	.02
Irritable	3.75	<0.001*	.27
Reckless	-4.82	<0.001*	-.34

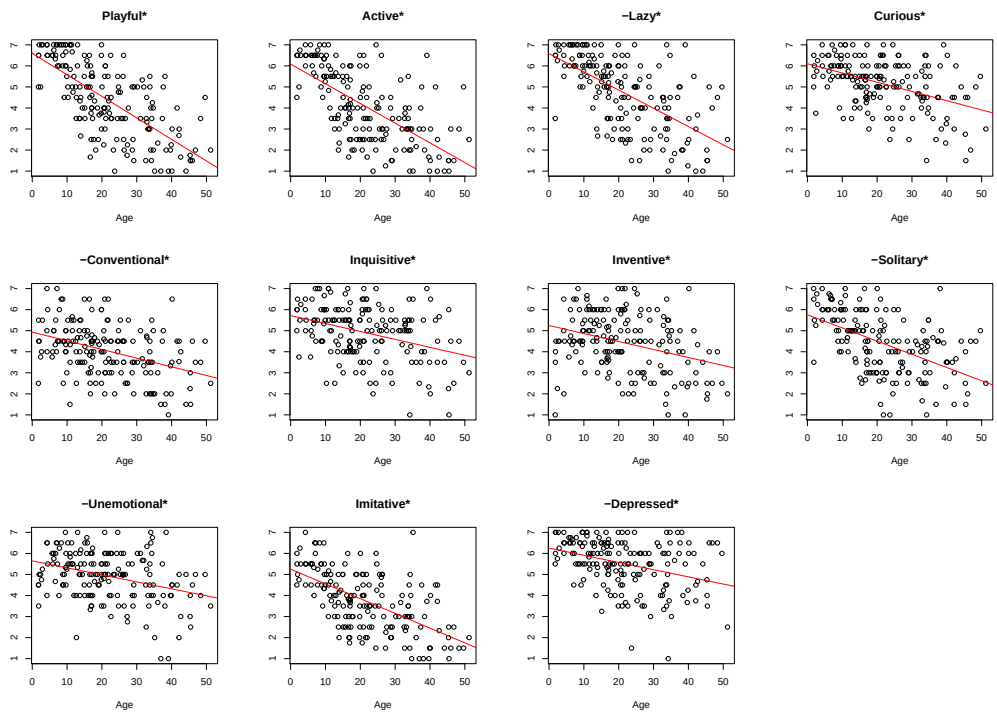

Figure 3.23: Correlations between age and extraversion items in orangutans using the OPQ.

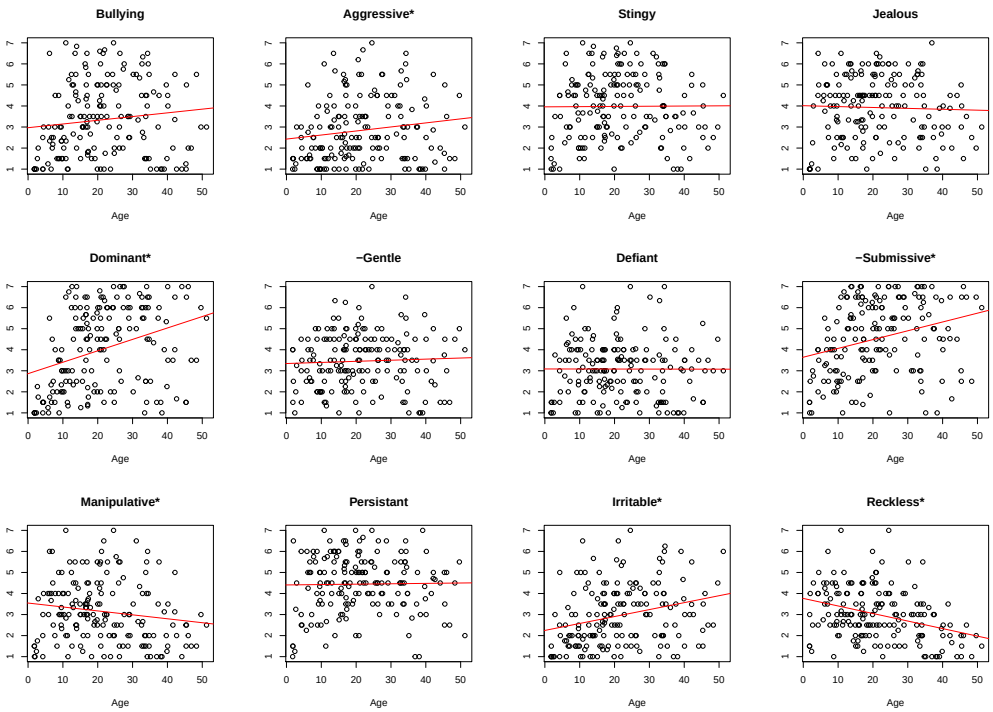

Figure 3.24: Correlations between age and dominance items in orangutans using the OPQ.

Table 3.21: Correlations between Orangutan Neuroticism and Age

Item	t-score	p-value	r
Anxious	-1.74	0.083	-.13
Fearful	-4.39	<0.001*	-.32
Cool(-)	-5.36	<0.001*	-.38
Timid	-1.69	0.092	-.13
Stable(-)	-3.26	0.001*	-.24
Excitable	-4.24	<0.001*	-.31
Impulsive	-3.18	0.002*	-.24
Cautious	1.16	0.249	.09
Vulnerable	-1.26	0.210	-.10
Erratic	-1.42	0.156	-.11
Predictable(-)	-4.00	<0.001*	-.29

Table 3.22: Correlations between Orangutan Agreeableness and Age

Item	t-score	p-value	r
Sympathetic	-0.74	0.459	-.06
Helpful	-1.67	0.097	-.13
Protective	2.80	0.006*	.21
Affectionate	-5.40	<0.001*	-.38
Sensitive	-0.47	0.636	-.04
Friendly	-6.64	<0.001*	-.45
Sociable	-6.83	<0.001*	-.46

Neuroticism Fearful, Cool, Stable, Excitable, Impulsive, and Predictable in the neuroticism domain all correlate negatively with age.

Agreeableness Affectionate, Friendly, and Sociable all show moderate negative correlations with age while Protective shows a weak positive association.

Intellect Moderate positive associations exist between age and the items Decisive, Independent,, ad Dependent while the item Disorganised shows only a weak correlation.

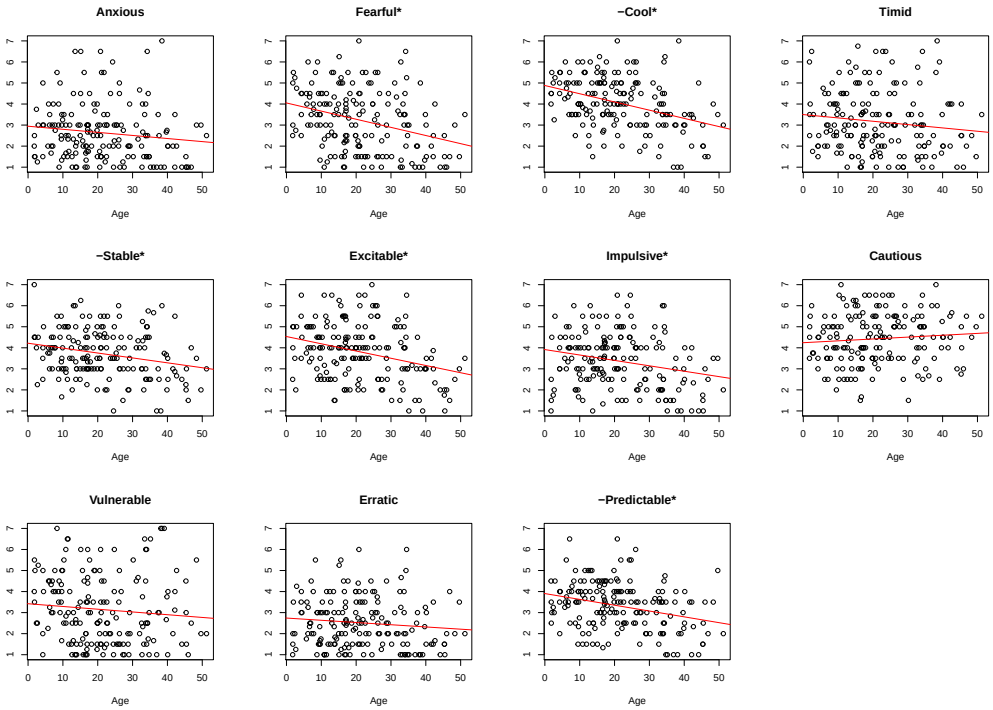

Figure 3.25: Correlations between age and neuroticism items in orangutans using the OPQ.

Table 3.23: Correlations between Orangutan Intellect and Age

Item	t-score	p-value	r
Intelligent	1.25	0.213	.09
Decisive	4.34	<0.001*	.31
Clumsy(-)	0.91	0.363	.07
Disorganised(-)	2.44	0.016*	.18
Independent	6.57	<0.001*	.45
Dependent(-)	9.04	<0.001*	.57

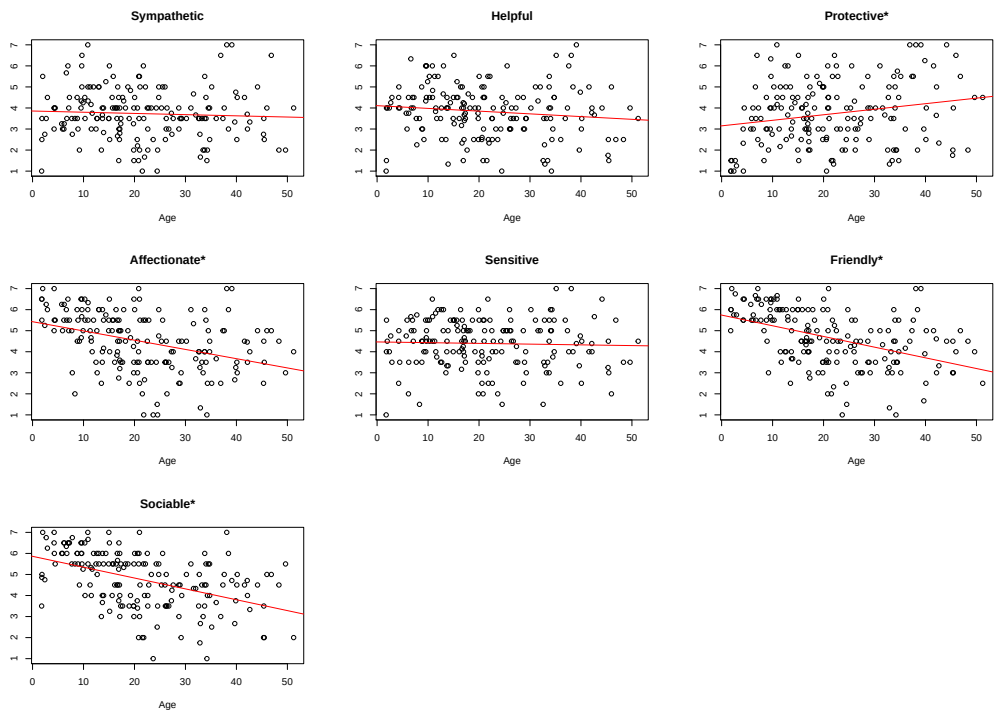

Figure 3.26: Correlations between age and agreeableness items in orangutans using the OPQ.

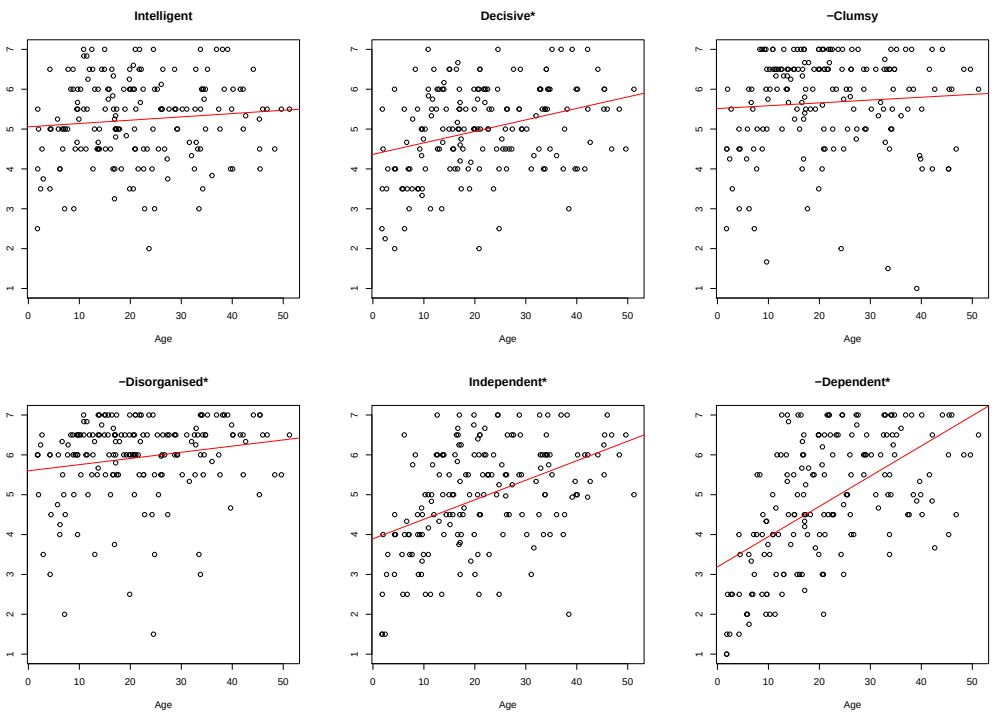

Figure 3.27: Correlations between age and intellect items in orangutans using the OPQ.

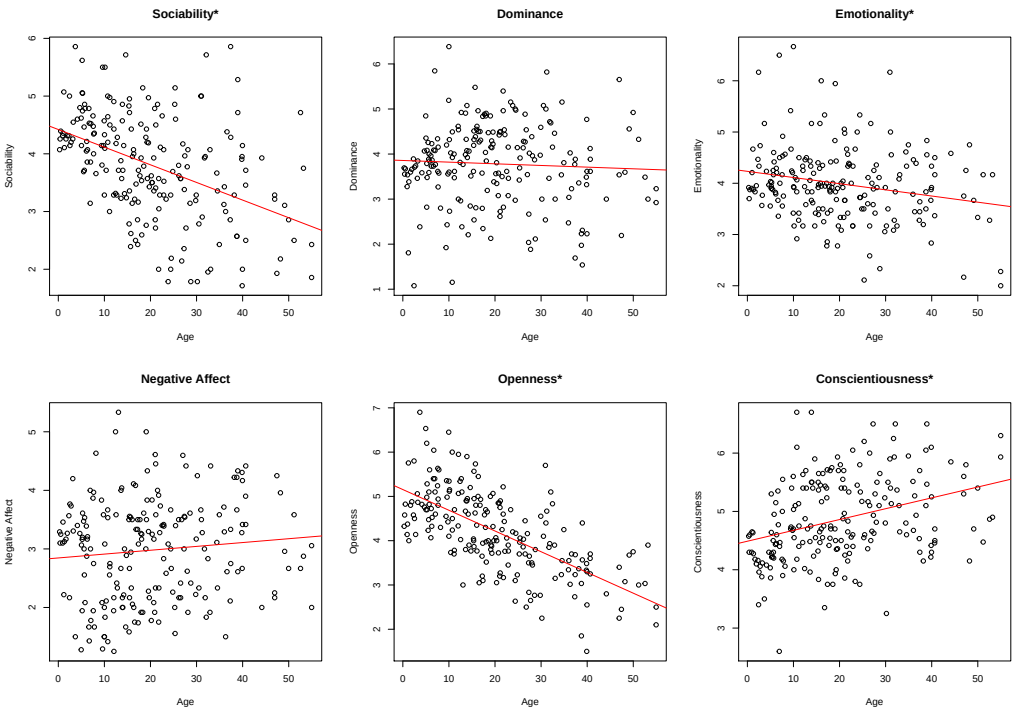

Figure 3.28: Correlations between age and factor scores in gorillas using the HPQ.

3.3.4 Gorillas

Of the six factors identified in captive gorillas, all but dominance (t=-0.76, p=0.450, r=-.05) and Negative Affect (t=1.42, p=0.157, r=.10) showed significant correlations with age. Sociability (t=-6.94, p<0.001, r=-.44), Emotionality (t=-3.15, p=0.002, r=-.22), and Openness (t=-12.25, p<0.001, r=-.65) all correlate negatively with age while Conscientiousness (t=5.07, p<0.001, r=.34) has a positive correlation with age.

Sociability All items in sociability correlate negatively with age except for Protective which does not correlate significantly.

Table 3.24: Correlations between Gorilla Sociability and Age

Item	t-score	p-value	r
Affectionate	-6.95	<0.001*	-.44
Sociable	-8.81	<0.001*	-.53
Sympathetic	-3.10	0.002*	-.21
Helpful	-3.58	<0.001*	-.24
Friendly	-6.79	<0.001*	-.43
Protective	0.88	0.386	.06
Dependent	-6.39	<0.001*	-.41

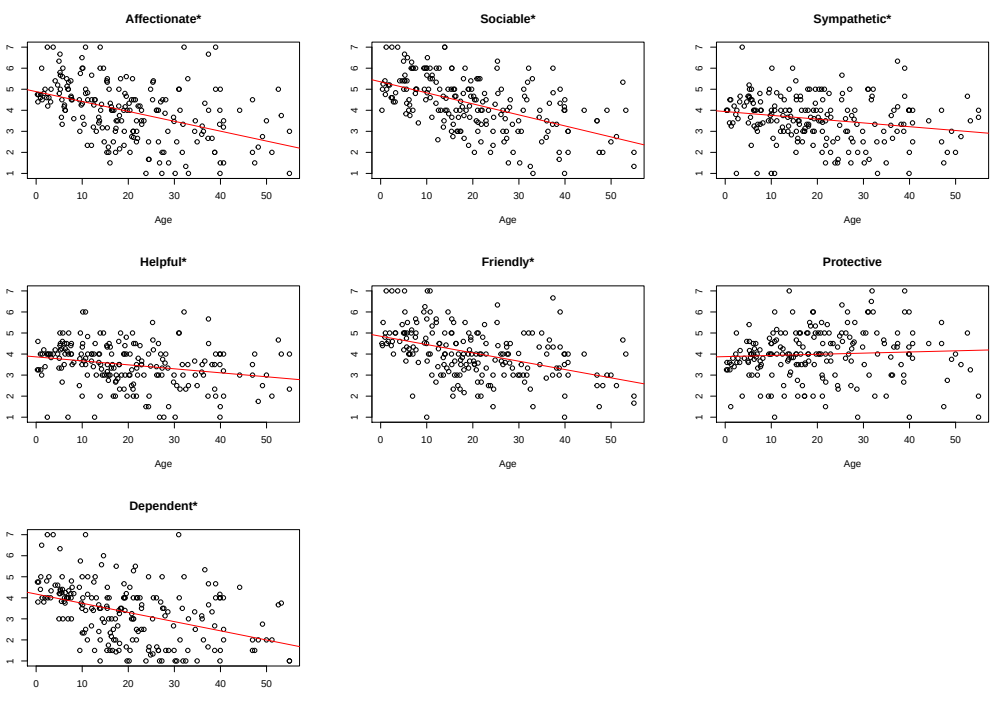

Figure 3.29: Correlations between age and sociability items in gorillas using the HPQ.

Table 3.25: Correlations between Gorilla Dominance and Age

Item	t-score	p-value	r
Stingy	0.562	0.574	.04
Dominant	2.17	0.031*	.15
Bullying	-1.39	0.165	-.10
Aggressive	-1.42	0.157	-.10
Jealous	-1.32	0.188	-.09
Submissive(-)	1.16	0.247	.08
Persistent	-1.06	0.292	-.07
Timid(-)	0.32	0.747	.02
Manipulative	-3.94	<0.001*	-.27
Gentle(-)	1.15	0.254	.08
Irritable	1.75	0.082	.12
Cautious(-)	-3.30	0.001*	-.23
Defiant	-3.58	<0.001*	-.25

Table 3.26: Correlations between Gorilla Emotionality and Age

Item	t-score	p-value	r
Cool(-)	-2.67	0.008*	-.19
Stable(-)	-1.03	0.304	-.07
Excitable	-0.99	0.323	-.07
Fearful	-1.39	0.167	-.10
Unemotional(-)	-2.03	0.044*	-.14
Independent(-)	-3.75	<0.001*	-.26

Dominance Only Dominant has a significant positive relationship with age. Manipulative, Cautious, and Defiant correlate negatively while the other items in the domain do not correlate significantly.

Emotionality Cool, Unemotional, and Independent all show weak negative correlations with age.

Negative Affect In negative affect Depressed and Solitary correlate positively with age while only Erratic associates negatively.

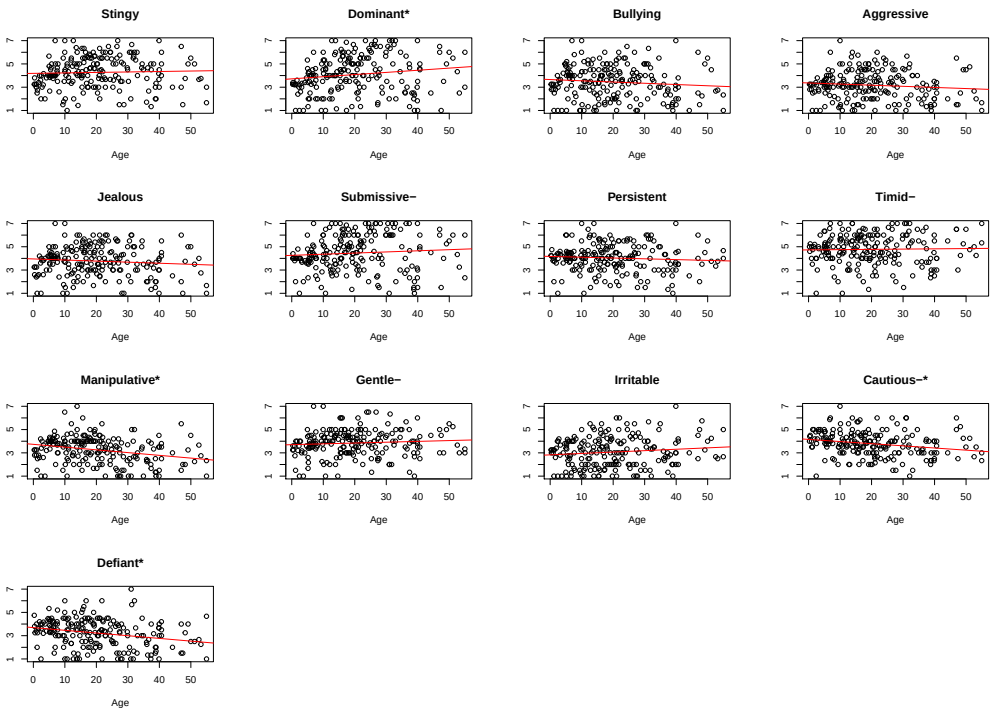

Figure 3.30: Correlations between age and dominance items in gorillas using the HPQ.

Table 3.27: Correlations between Gorilla Negative Affect and Age

Item	t-score	p-value	r
Depressed	2.56	0.011*	.18
Solitary	7.86	<0.001*	.48
Autistic	0.55	0.580	.04
Anxious	-0.96	0.339	-.07
Erratic	-2.88	0.004*	-.20
Vulnerable	-1.32	0.187	-.09

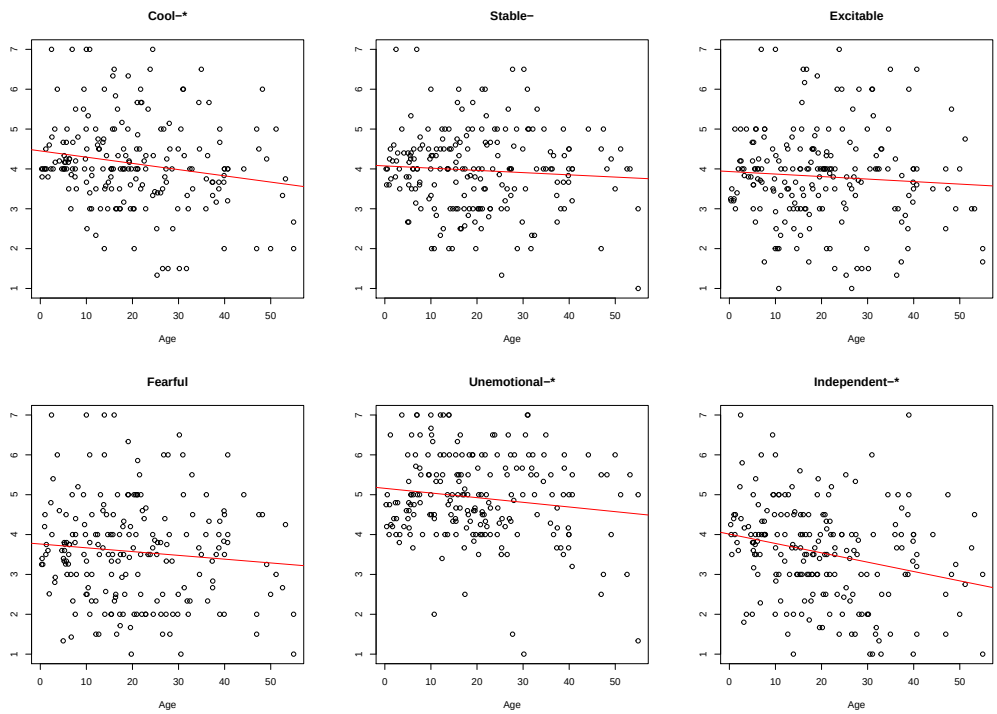

Figure 3.31: Correlations between age and emotionality items in gorillas using the HPQ.

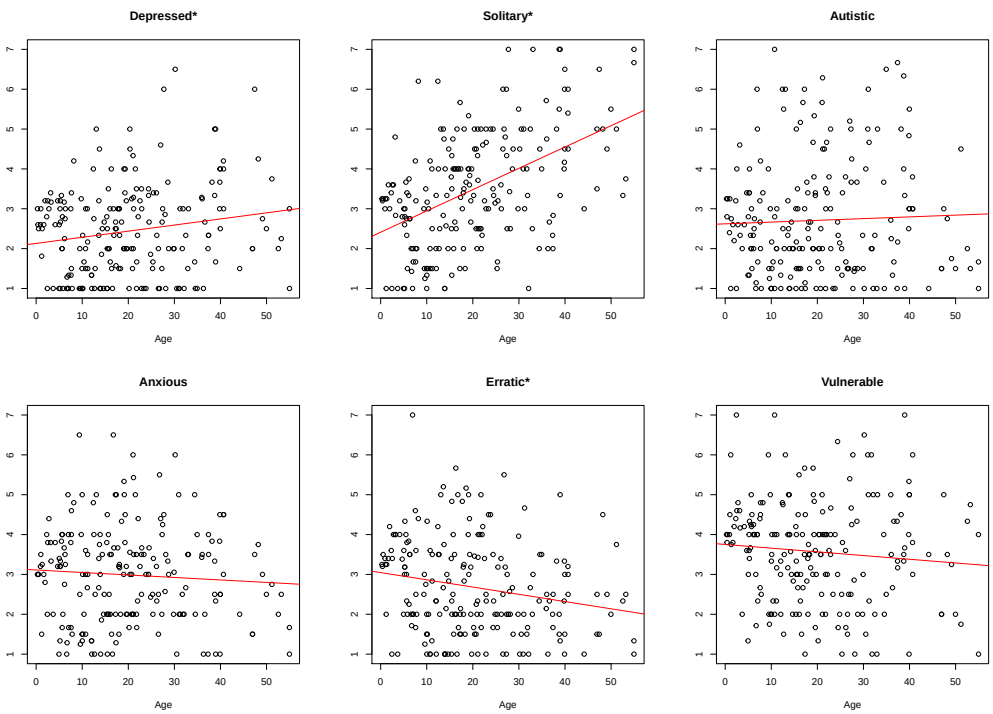

Figure 3.32: Correlations between age and negative affect items in gorillas using the HPQ.

Table 3.28: Correlations between Gorilla Openness and Age

Item	t-score	p-value	r
Innovative	-6.90	<0.001*	-.44
Inventive	-7.07	<0.001*	-.45
Inquisitive	-7.46	<0.001*	-.47
Curious	-6.50	<0.001*	-.42
Conventional(-)	-5.49	<0.001*	-.36
Active	-13.89	<0.001*	-.70
Individualistic	-0.70	0.483	-.05
Imitative	-9.52	<0.001*	-.56
Playful	-13.92	<0.001*	-.76
Lazy(-)	-9.24	<0.001*	-.55

Table 3.29: Correlations between Gorilla Conscientiousness and Age

Item	t-score	p-value	r
Disorganised(-)	3.83	<0.001*	.26
Intelligent	1.44	0.152	.10
Unperceptive(-)	1.37	0.174	.10
Clumsy(-)	2.80	0.006*	.19
Thoughtless(-)	4.38	<0.001*	.30
Distractible(-)	5.08	<0.001*	.34
Decisive	2.76	0.006*	.19
Sensitive	0.59	0.556	.04
Predictable	5.81	<0.001*	.38
Reckless(-)	5.41	<0.001*	.36

Openness All items in openness show moderate to strong negative correlations with age while only Individualistic does not vary significantly.

Conscientiousness All items in conscientiousness except for Intelligent, Unperceptive, and Sensitive show significant positive correlations with age. These three do not vary significantly.

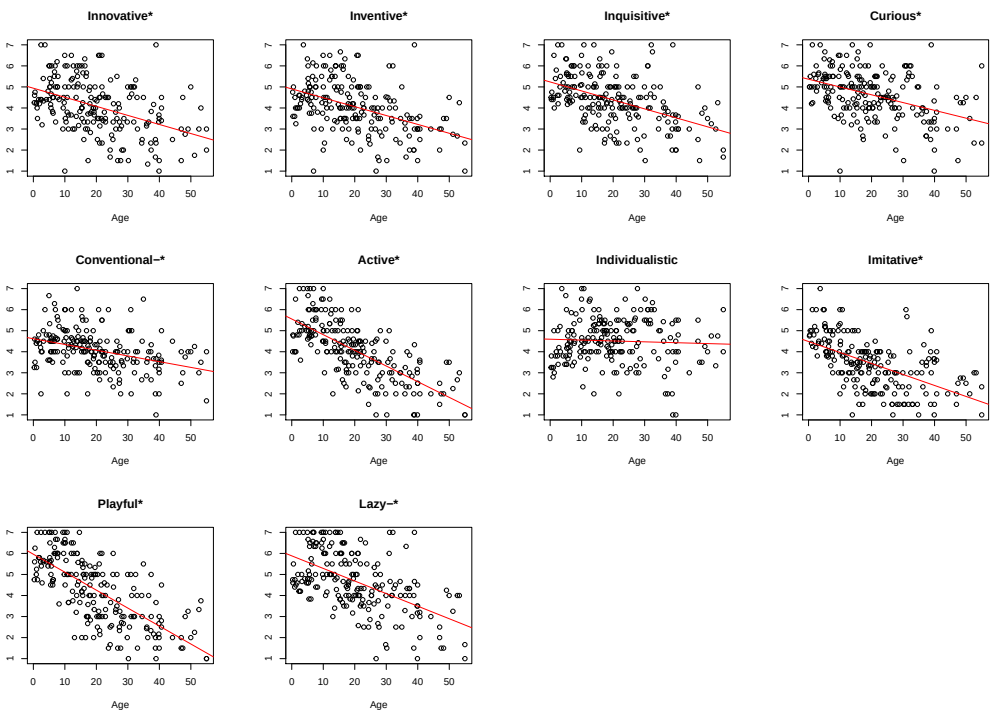

Figure 3.33: Correlations between age and openness items in gorillas using the HPQ.

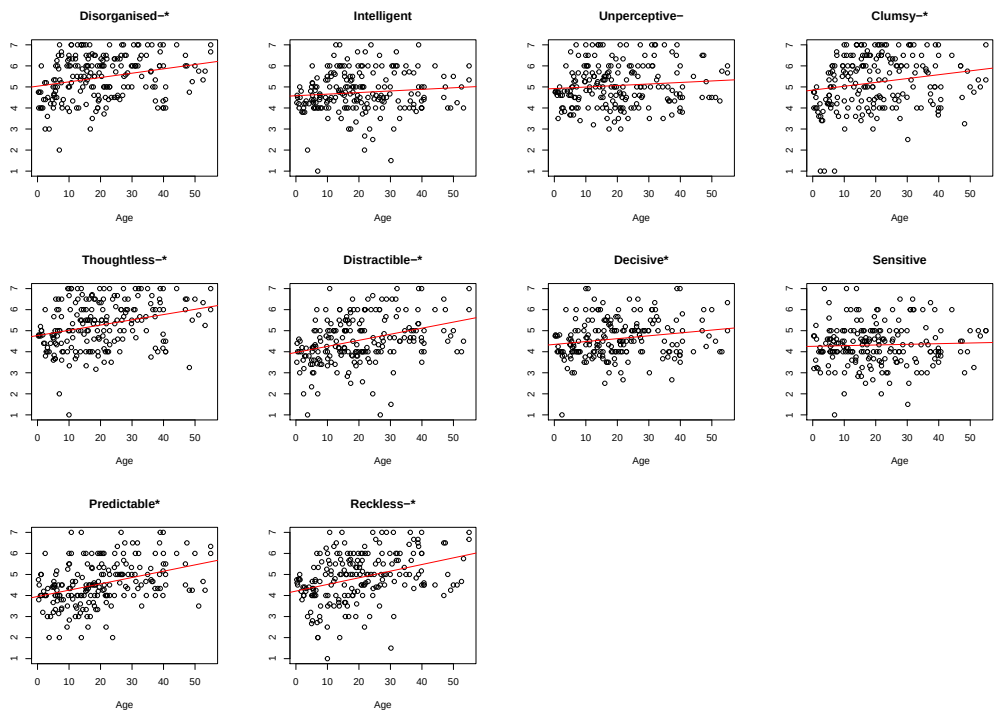

Figure 3.34: Correlations between age and conscientiousness items in gorillas using the HPQ.

3.4 Discussion

3.4.1 Chimpanzees

CPQ At the factor level, we can see that only three of the factors show any changes with age. Extraversion and openness seem to decrease while higher dominance is associated with old age.

Looking at extraversion, we see that at the nuance level every item decreases with age. They do not all vary to the same degree however. Items such as Active, Playful, and the inverted item Lazy show quite steep declines between -.60 and -.70 while others such as Affectionate, Friendly, and Depressed have a much weaker association with age, around -.20. The uniformity in significance and direction of these item correlations contributes to the strength of the overall factor correlation which is the highest association seen in the species.

Conscientiousness as measured by the CPQ does not correlate significantly with age at the factor level, though more than half of its contributing items do show some change. Predictable, and the negatively scored Impulsive, Reckless, and Jealous all show weak positive relationships while Irritable bucks the trend with a slight negative correlation. The remaining four reverse scored items, Defiant, Erratic, Aggressive, and Disorganised, all show no change with age.

Though two out of the three items that make up neuroticism in the CPQ show significant variation with age, the overall factor does not. The reverse scored Stable shows a weak negative relationship while Unemotional shows the opposite, a weak positive relationship. The final item, Excitable, does not change with age.

In Agreeableness only one item shows any significant relationship with age. The item Protective has a weak negative correlation with age while the other

items, Sympathetic, Helpful, Sensitive, and Gentle, all follow the trend of the factor and remain consistent across the age range.

Openness in the CPQ also seems to follow the trend of extraversion where all of the contributing items follow the direction of the overall factor. This is explained somewhat by the fact that here openness is only measured by two items. Inquisitive and Inventive both have negative relationships with age, the former slightly stronger than the latter at -.39 and -.28 respectively.

Dominance, the largest factor in chimpanzee personality, has a small positive correlation with age at the factor level which appears to be driven by just over half of its items. The strongest association with age out of these items is Dependent which is reverse scored and has a correlation of .32. Most of the remaining significant relationships with items, Dominant, Independent, Decisive, and negatively scored Submissive, and Fearful, are weak positive correlations. There is one exception however, scores on the item Stingy appear to decrease slightly with age against the grain of the overall factor relationship. The remaining items Intelligent, Persistent, Bullying, and the inverse of Timid and Cautious show no significant variation with age.

HPQ With the expanded HPQ, we see the same pattern of factor variance with age albeit with some small differences in the magnitude of the relationships. Extraversion still has a strong positive relationship with age while openness and dominance maintain their weak negative associations through the addition of new items. Conscientiousness, neuroticism, and agreeableness also maintain their consistency and continue to show no change with age.

Extraversion in the HPQ does not show the same united front present in the CPQ item, though the patterns are largely the same. Active, Playful, and

negative Lazy still hold their large negative correlations with age and the same goes for the smaller correlations of Sociable, Imitative, and Solitary. A few of these items have slipped below the threshold of significance however. In the HPQ weak associations with age seen in the items Friendly, Affectionate, and Depressed are not present and no relationship exists in the newly added item Individualistic.

Conscientiousness continues to show no changes with age and in the HPQ only three items have significant relationships. The only positively scored item in the factor, Predictable, has a moderate increase with age, echoed by increases the negatively scored items Thoughtless and Distractible though these are smaller in magnitude. The remaining eleven items show consistent scores across the age range and do not vary.

In the HPQ the composition of the factor neuroticism changes quite dramatically from the CPQ. Unemotional no longer has a significant loading on any factor in this scale and two new items, Autistic and Cool, are added. Nevertheless neuroticism maintains its temporal stability and continues to show no changes with age at the factor level. On the item level however, only the reverse scored item Cool shows a weak negative association with age. The other items, Excitable, Autistic, and the negatively scored Stable all show no change.

Agreeableness also holds fairly consistently to the pattern seen in the same CPQ factor. Again only one item shows a relationship with age however here it is the new item Conventional which has a positive correlation. The other five items, Sympathetic, Helpful, Sensitive, Protective, and Gentle, all do not correlate significantly with age.

Openness is the only factor in the HPQ to maintain its trend from the CPQ

of all contributing items showing significant correlations in the same direction as the overall factor. The four items associated with openness, Inquisitive, Inventive, Curious, and Innovative, all have moderate negative relationships with age which mirror the moderate negative relationship of the overarching factor.

Still the largest factor, we see the same pattern again in dominance where the overall factor correlation with age is driven by several item level correlations. Apart from Dependent which has a moderate relationship with age, all of the significant items Dominant, Independent, and the negatively scored Submissive, Fearful, and Timid have small positive correlations with age. The remaining items, Decisive, Intelligent, Persistent, Bullying, Stingy, Manipulative, Cautious, Vulnerable, and Anxious, all have no association with age.

3.4.2 Bonobos

In bonobos, three factors show significant variation with age. Extraversion and openness both decrease with age while agreeableness increases. As in chimpanzee, we can see that these changes are driven by specific item level variation.

The negative relationship between extraversion scores and age in bonobos appears to be driven by only one item out of the four negatively scored items comprising the factor. Solitary has a moderate negative correlation with age while Depressed, Autistic, and Individualistic all show no significant change across the age range.

Conscientiousness shows no change with age and this is echoed, with a few exceptions, in its constituent items. The only items that show any significant variation with age are two positive relationships with Reckless and Impulsive

and one negative one with Irritable. All of these items are reverse scored and the magnitude of the correlations is relatively small. The remaining nine items that make up conscientiousness in bonobos show no associations with age.

Attentiveness also has no overall change with age and the items contained within it reflect this with one exception. The reverse scored item Distractible does have a small positive correlation with age but Disorganised, Intelligent, Clumsy, Thoughtless, and Unperceptive all do not change with age.

The factor of agreeableness shows another interesting continuation of a trend where the overall significant factor correlation with age is driven by correlations in a minority of items. Here the items Protective, Sympathetic, and Sensitive all have weak to moderate (.26 to .37) positive relationships with age and which are responsible for the overall weak association of the factor. The majority of items, Friendly, Affectionate, Helpful, and Sociable, have no significant correlation with age and appear to stay consistent across the lifespan.

Counter to the aforementioned trend of minority rule, the items in openness show clear support for their associated factor. All of the items which make up openness in bonobos show negative associations with age. Some of these correlations are remarkably strong (e.g. Active at -.73 or Imitative at -.54) and this contributes to the overall moderate negative correlation of -.41 between openness and age.

The largest factor in bonobos, assertiveness, shows no relation to age. There are however, several items contained within which do. Dominant, Independent, and the reverse scored Dependent and Submissive all show positive associations with age that do not coalesce at the factor level. This may be due in part to the other nine items which have no significant correlations with age.

3.4.3 Orangutans

In orangutan personality four of the five factors show significant variation with age. Only dominance appears to remain consistent across the lifespan.

Extraversion in orangutans has the highest magnitude negative correlation with age seen in this study, which is not surprising when looking at the association of the items comprising this factor. All eleven of the constituent items possess significant negative correlations with age. These correlations range in strength from -.34 for the reverse scored item Unemotional to the very high -.69 for the item Playful.

Dominance, the only factor that does not vary with age, still has several items within it that do correlate. Positive relationships exist between age and the items Aggressive, Dominant, Irritable, and the reverse scored Submissive while the items Reckless and Manipulative are negatively correlated. The remaining items Bullying, Stingy, Jealous, Defensive, Persistent, and the negatively scored Gentle all have no relationship with age.

The overall negative relationship with neuroticism is driven by the items Fearful, Excitable, and the reverse scored Cool, Stable, and Predictable which all correlate negatively with age. The remaining items of Anxious, Timid, Cautious, Vulnerable, and Erratic all show no change with age.

Agreeableness has an overall negative relationship with age that is driven by three moderately negative correlations between age and the items Affectionate, Friendly, and Sociable. One more weak correlation exists within the domain between Protective and age as well. The items Sympathetic, Helpful, and Sensitive all do not have any significant relationships with age.

Intellect is the only orangutan domain that shows an increase with age and this is driven by a few items associated with it. Decisive, Independent, and

the reverse scored Dependent all have moderate correlations with age while the negatively scored item Disorganised has a weak positive correlation. The remaining items Intelligent and reverse scored Clumsy both do not vary with age.

Comparing these results to the findings of King et al. (2008), we see that they are similar on the overlapping domain levels and that the item-level analysis provides greater context and detail. Looking at extraversion in chimpanzees, we see that the same negative association with age is seen in these data. Though the data used in that study is also included in the present analysis, our larger datasets help to reinforce their findings. They also found that, when looking at the two facets described in their paper, these lower order personality levels mirrored the negative associations seen at the factor level. Using the CPQ, we see a complete following of the factor trend with all of the individual items correlating negatively with age, matching the previous findings. In the HPQ we see more variation in item associations with not all of the items showing significant variation but overall the trend matches the decrease with age of the factor. There is less agreement when looking at the facets as defined by King et al. (2008). In their 'gregarious' facet they found an overall negative association with age but looking at the item level we can see that only four out of the seven items show this decline (Playful, Sociable, Affectionate, Imitative, Friendly, Solitary, and Depressed). Their second facet of 'activity' is a bit more clear cut as both items (Active and Lazy) match the overall significant decrease with age in the facet.

Looking at their other faceted domain, conscientiousness, reveals a more complex picture. At the factor level, both studies did not see a significant variation with age in conscientiousness. In the present study this applies to

both the CPQ and the HPQ data. Using the facets as described by King et al. (2008), we see that both increase significantly over the age groups used in the study. Of the items contained in their facet 'predictability,' Predictable, Impulsive, Reckless, Erratic, and Disorganised, just over half show this positive change with age. Interestingly, in this study the CPQ items identified as part of the 'tameness' facet, Defiant, Irritable, Aggressive, and Jealous, here do not seem to match the pattern seen in their study. Only Jealous shows a significant increase with age while Irritable actually shows the opposite relationship. When taking the full HPQ into account, only the item Predictable shows any change with age of the 'predictability' facet and none of the 'tameness' items vary with age.

The remaining factors were only assessed at the domain level. Agreeableness and neuroticism in our study were not significantly correlated with age, though several included items were, and in the King et al. (2008) study significant correlations were only found with the exclusion of the youngest of their age groups. Openness did show a significant decline with age between the two studies and also in both of the measures used here. Dominance in both studies and across both measures showed a significant increase with age.

It is also important to compare between the nuance level examined here and the findings of Weiss and King (2015) who investigated age differences in chimpanzees and orangutans. Again there is overlap between the datasets used in both studies but the addition of detail provided by the item-level analyses still allows for a more intricate understanding of developmental personality in nonhuman apes.

For the chimpanzee data in that study, we see the same patterns emerging as in the King et al. (2008) study. The orangutan analyses tell a different

story however. Looking at extraversion in orangutans, at the factor level we see declines with age in both studies and a similar pattern in the facets defined by Weiss et al. (2006). These are the same as those earlier described in chimpanzees and the negative associations with age continue down to the item level where all items that make up orangutan extraversion significantly decline with age.

Other comparable factors were also analysed and showed largely similar trends to what is seen in the present study. Dominance increased in both species in that study and looking at the items we can see that this was driven by a few specific items in both species, particularly Dominant and Submissive. The increase in dominance in orangutans was not seen here, though this may be due to that fact that it would appear to increase and then decrease when analysed in blocked age groups, potentially negating overall age-related changes. Neuroticism was seen to decline in both species (King et al., 2008; Weiss & King, 2015), a pattern which was not replicated in chimpanzees in the present study. These changes are driven by variation in specific items which do show change across the species but are associated with different factors in different measures. Some examples of these items are Stable, Cool, Fearful, and Predictable. In agreeableness again we did not find a comparably significant different in chimpanzees but did in orangutans, again driven by a few common items such as Protective, Friendly, Affectionate, and Sociable (though the latter three are contained in extraversion in chimpanzees). Interesting to note is that these changes are not all seen in the HPQ data, with only Sociable varying with age here. Finally we see the same increase in the orangutan domain intellect in both studies. This is driven by the items Decisive, Disorganised, Dependent, and Independent, of which the latter two vary with age in both

chimpanzee measures as well.

3.4.4 Further Validation of Nuances in Nonhumans

One of the potential drawbacks of this application of nuance level analysis is the lack of verification by the criteria outlined by Mõttus et al. (2017). This also highlights a clear path for future research. Specifically, the next steps would look at providing supporting evidence from multiple measures, stability over time in a longitudinal study, and the identification of the genetic foundation of the nuance level personality in nonhuman apes.

To address the issue of stability over time, a longitudinal study of personality using these questionnaires would be fairly straightforward to undertake. The main problems with this are logistical, as completing these questionnaires can only be done by a specific group of caretakers, researchers, and volunteers at each facility and completing several 54 item questionnaires on top of the everyday workload of a zookeeper or primate researcher can be time consuming. There is also the question of value of data, if only one new dataset can be collected, is it better to get personality data on a new species and expand the scope of the field or to collect more data on the same individuals for this longitudinal study? Up to this point the former has been the option preferred by researchers but the longitudinal work may become more attractive in the near future.

In previous studies it has been shown that nonadditive genetic effects such as dominance play a large role in personality variation in humans (Pilia et al., 2006), suggesting influence from balancing selection (Penke et al., 2007a) and/or life-history traits (Figueredo, Gladden, Vásquez, Wolf, & Jones, 2009) on the evolution of these traits (for a review see Chapter 1). In studies inves-

tigating the genetic basis of personality in nonhumans, dominance has been shown to be heritable in chimpanzees (Weiss et al., 2000) and further genetic variation has been shown in orangutans (Adams, King, & Weiss, 2012), the majority of which is nonadditive. This suggests that selection on these personality traits has been long-term directional or stabilising since the great apes shared a common ancestor (Adams et al., 2012). This provides a strong starting point for the investigation of the genetic foundation of personality as a whole in nonhuman great apes but still falls short of the criterion set out by Mõttus et al. (2017). To be confident in a specific assessment of the genetic factors related to nuance-level analysis in these species, again more data must be collected. In this case, acquiring pedigree data on the individuals assessed in this study is the simplest solution as this data is maintained by zoos and care facilities and is much more realistically accomplished than genetic sequencing of all of these individuals. Most researchers studying human personality genetics, including Mõttus et al. (2017), use data on twins to assess genetic influences. While a twin study of a useful magnitude in other great apes would most likely be impossible even with a sample of every living ape, assessing relatedness and heritability through pedigree can potentially make up for this lack of twins and provide a method for further supporting the item-level genetic foundation of nonhuman personality.

Looking at a validation through multi-measure approaches is more difficult in nonhumans than in humans for a number of reasons, not least of which being that the primary source of human personality data, the self-report questionnaire, is unavailable in these cases. We must then be more creative in our assessments to accomplish this particular goal of validation. The most direct comparisons may be the closest in format to the primary data used here.

Other personality questionnaires looking at nonhuman personality have been developed independently from the HPQ and these can potentially be used to investigate patterns of change over time in similarly defined constructs. One such independent questionnaire is that developed by Dutton, Clark, and Dickins (1997). Here, following the constructivist approach of Kelly (1955), each rater in the study generated pairs of bipolar dimensions which were unique to the rater and later correlated with each other in the final analysis. Using alternative methods of assessment such as this can help identify more general trends in the underlying development of personality. Another method of assessment that can be used in comparative validation studies is behavioural assessment. There are various ways personality can be assessed through behaviours (S. D. Gosling, 2001) and using these methods would provide an even greater degree of independence, considering raters in the HPQ and related measures are explicitly instructed not to focus on specific instances or frequencies of behaviours when completing the questionnaires. There are drawbacks to these methods however and again logistics plays no small role in the limitations. Collecting large amounts of behavioural data on apes where introduction to unfamiliar environments makes up an important part of the assessment is quite difficult and future behavioural comparisons may have to make use of more non-invasive observational techniques.

3.4.5 Future Analyses

Beyond further verification of the nuance hierarchical level, the next obvious step in research is the application of these idea to areas where greater predictive utility will be beneficial. Though several of the outcomes used in nuance research in humans are not directly applicable here, such as political beliefs

(Mõttus et al., 2017), a survey of the current body of research in nonhuman personality reveals welfare and well-being as two major areas which could benefit from this analysis. Several studies have linked personality traits to welfare (e.g. Herrelko, Vick, & Buchanan-Smith, 2012; Tetley & O'Hara, 2012) and to subjective well-being (e.g. Suomi & Novak, 1991; Weiss et al., 2002, 2006; Weiss & King, 2007; Weiss, Adams, Widdig, & Gerald, 2011; Lee & Moss, 2008; M. C. Gartner & Weiss, 2013) in a wide variety of species. In all of these situations lies the potential for increased accounting for specific variance provided by these nuances. All or part of the effects observed in these studies may in fact be driven by a few specific items, as is the case for age in many of the nonhuman ape personality factors and especially in comparisons with things like welfare and well-being attributing effects from a few specific items to facets or factors as a whole may be misleading with respect to the mechanism underlying the associations. Mõttus (2016) even goes so far as to suggest that testing whether facet or domain level relationships are instead a result of specific items or nuances should become standard practice in personality research. Whether this idea is taken up in the primate personality research community, or even the individual differences community at large, there are certainly instances in nonhuman research where these types of analyses may be useful in predictive capacities.

Chapter 4

The application of the Hominoid Personality Questionnaire (HPQ) for use in ring-tailed lemurs (*Lemur catta*)

4.1 Introduction

The family *Lemuridae*, known collectively as lemurs, can trace its origins to the early primate branch *Adapiformes* (Kay et al., 1997), diverging from the *Omomyformes* which later became tarsiers, apes, and monkeys somewhere around 68.7 million years ago (mya, Perelman et al., 2011). *Lemuriformes* make up one half of the families in the primate suborder *strepsirrhini*, along with *lorisidae*, and colonised the African island of Madagascar some 58.6 mya (Perelman et al., 2011). The exact mechanism of this colonisation has been studied for decades and several theories have been proposed including now-

submerged land bridges and improbable "sweepstakes" crossings of the Mozambique Channel made more probable by the vastness of geologic and evolutionary time (Wallace, 1892; Simpson, 1940; Stankiewicz, Thiart, Masters, & De Wit, 2006). While the divergence date is quite convincingly estimated by molecular phylogenetic analysis (Perelman et al., 2011), the most recent theory of how these primates crossed the sea is via a series of small island that have since been submerged in a sort of leapfrogging fashion before arriving on Madagascar in sufficient numbers to support a breeding population (Stankiewicz et al., 2006; Mazza, Buccianti, & Savorelli, 2019). Whatever the method, once the early lemurs arrived on the island, they rapidly radiated outwards to fill an impressive variety of ecological niches from the tiny cyanide-defying bamboo lemur (Glander, Wright, Seigler, Randrianasolo, & Randrianasolo, 1989) to the extinct sloth lemur which weighed on average 160kg (Godfrey, Jungers, & Schwartz, 2006; Jungers, Demes, & Godfrey, 2008).

Today the only wild members of the *Lemuridae* family are the over 100 species and subspecies of lemur that live in Madagascar and they are the only primates to inhabit the island (Richard & Dewar, 1991; Mittermeier et al., 2008). Apart from their geographic isolation, lemurs share several characteristics that differentiate them from their other primate relatives. On average, lemurs tend to display reduced or non-existent levels of sexual dimorphism (van Schaik & Kappeler, 1993). Most lemur species associate in male-female dyads but the species that congregate in larger social groups tend to be matrilineal with male dispersal and female social dominance (van Schaik & Kappeler, 1993).

In this study, we focus on the best known and most well researched species of lemur, the ring-tailed lemur (*Lemur catta*). In the wild ring-tailed lemurs live

mostly in the dry deciduous forests and spiny brush of southern and southwestern Madagascar (Goodman, Rakotoarisoa, & Wilmé, 2006). They are highly adaptable and have also branched out into high mountain ecosystems and anthropogenic grassland (Goodman et al., 2006). They live in small social groups of around five to ten individuals. These groups are female dominated and consist of one (or more rarely two) core matrilineal families of adult females and their offspring and one or more central males (Gould, 2006). Male offspring and peripheral males disperse at maturity and sometimes will become members of several groups over their lifespans. When a group becomes larger than around fifteen to twenty-five individuals, several subordinate females will be pushed out of the group to split off and form a new group (Jolly et al., 2002). Their diets are largely seasonal in the wild and are omnivorous, feeding on fruit, leaves, flowers, insects, and occasionally small birds or lizards (Simmen et al., 2006). Sexual maturity in both males and females comes around three years of age and mortality usually occurs between ten and fifteen years, though some individuals have been recorded living as long as nineteen years (Gould, 2006).

Lemurs as a whole utilise scent marking and olfactory signals for communication and ring-tailed lemurs are no exception. Using scent glands on their genitals and also on their forearms in males, ring-tailed lemurs leave identifiable scent marks in specific, repeated locations (Oda, 1999). The purpose of these signals is to demarcate territory and also as a form of long-distance communication, correlating with dominance status and inversely with long-range contact call production in a highly individualistic way (Oda, 1999). These calls are used as a way of maintaining group cohesion when the group is dispersed while scent marks are used when the group is closer together. These cross-modal

messages help to bolster communication within the group. Another communication method relevant to the present study are the dominance related squeals expressed by male ring-tailed lemurs. Squeals are forceful short-range vocalisations and are used by lemurs to assert social dominance over other males in the separate male dominance hierarchy within a group (Bolt, 2013). Together these and other communicative behaviours reinforce the status of ring-tailed lemurs as the most gregarious of the lemur species (Jolly, 1966).

While alone on the island for tens of millions of years, the Madagascan lemurs were joined by another primate species around the year 400 BCE (Blench, 2007). Modern humans have evolved from that other branch of early primates, the *Omomyformes*, and have developed highly complex cognitive capacities and social groups which allowed them to become both highly adaptable and highly successful around the globe (Wrangham, 1987; Hills, 1992). One key aspect of this relevant to the current study is the set of predictable behaviours and inherent characteristics known as personality (Digman, 1990).

In the modern scientific context, personality as we know it has been studied for over 130 years since Sir Francis Galton began his investigation into the measurement of character in man (Galton, 1884). He found that the most important individual differences were often incorporated in single words and proposed that the tools for measuring personality already existed within human language. Known as the lexical hypothesis, this idea has formed the bedrock of personality research. Allport and Odbert (1936); Allport (1937) attempted to define a system of codification for personality by collecting vast numbers of descriptive adjectives to begin the process of transferring the theory of the lexical hypothesis into practice. Following up on this, Raymond R. B. Cattell (1943, 1946, 1947, 1948) reorganised these lists into a much more manageable

171 descriptive terms to which he then applied factor analysis and other multi-measure techniques to develop his set of sixteen primary personality traits (R. B. Cattell et al., 1957).

Cattell's was not the only set of traits to be derived from vocabulary lexica however and, through a large and diverse body of research (for a review see Digman, 1990), two other personality structures emerged. These were the three-factor theory of H. J. Eysenck and Eysenck (1964) and the five-factor structure of Goldberg (1990). In this study we will focus on the latter and more specifically the branch of the academic phylogeny containing the work of Paul Costa and Robert McCrae.

Costa and McCrae are responsible for the development of the widely used five factor personality measure known as the Neuroticism, Extraversion, Openness Personality Inventory (Costa & McCrae, 1985, 1992). This is a self report, five-point Likert scale questionnaire used to assess personality based on the Five-Factor Model (FFM, McCrae & John, 1992). Here, personality adjectives are divided based on factor analysis into five bipolar spectra known as personality traits (McCrae & Costa, 1999). These factors are extraversion, neuroticism, conscientiousness, agreeableness, and openness to experience (Costa & McCrae, 1985).These traits are stable, reliable, and consistent across ages and cultures in humans (Costa & McCrae, 1986; Costa et al., 1986; McCrae & Costa, 1987; McCrae, Zonderman, Bond, Costa, & Paunonen, 1996; McCrae & Costa, 1997b).

In much the same way as we can judge physical traits that have evolved through an examination of the phylogenetic tree, so too can we examine the evolutionary history of personality by looking at personality in different species (S. D. Gosling & Graybeal, 2007; Harvey & Pagel, 1991). King and Figueredo

(1997) began looking at personality in the closest living relative to humans, chimpanzees. Using 41 items borrowed from Goldberg's (1990) Five-Factor Model and two of their own (Clumsy and Autistic) they created the Chimpanzee Personality Questionnaire (CPQ, King & Figueredo, 1997). By applying similar factor analytic techniques as Goldberg (1981) and McCrae and Costa (1985) they identified six personality factors. The first five are similar to the five found in humans and later the same labels as the human traits were applied to aid comparison (King et al., 2005). The sixth is a trait not seen in humans and, as it governed tendencies to act dominant in social situations, was named dominance (King & Figueredo, 1997). The data for these studies was collected from observer report questionnaires from multiple familiar observers. Subsequently it has been shown that personality traits in nonhuman primates are reliable and consistent across both raters and time (King & Figueredo, 1997; King et al., 2008; Stevenson-Hinde et al., 1980a; Uher, Asendorpf, & Call, 2008; Weiss & King, 2006), valid against other measures such as observed behaviour (Capitanio, 1999; Konečná et al., 2008; Pederson et al., 2005; Uher & Asendorpf, 2008), and are not anthropomorphic projections (Weiss et al., 2012).

Branching out from this research, Weiss et al. (2006) applied the same idea to personality in orangutans. Adding several items to the initial questionnaire to better represent neuroticism and openness in orangutans as compared to chimpanzees (Weiss et al., 2006), five personality factors were identified in orangutans. Notable here is the continued presence of a dominance trait and a reduced emphasis on openness and conscientiousness to the point where these two traits have merged into one, labelled intellect. After this point, to better facilitate comparison and to be more representative of the full suite of person-

ality, Weiss et al. (2009) added more items to create the more widely applicable Hominoid Personality Questionnaire (HPQ). This measure consists of 54 items and has also been shown to be reliable, valid, and consistent in its identification of personality factors in chimpanzees (Weiss et al., 2009, 2012). This version of the questionnaire was used to identify the personality structure in bonobos (Weiss et al., 2015) and gorillas (Eckardt et al., 2015, Baur, in prep) as well as other more diverse species like rhesus macaques (Weiss, Adams, Widdig, & Gerald, 2011).

It is from this slightly modified version of the HPQ that we make our leap to the study of personality in lemurs. Rhesus macaques are quite substantially different from the apes in their behaviour and social structure. They live in multi-male, multi-female groups which are matrilineal (Melnick & Pearl, 1987) in which it is the males who disperse and the females who stay as the group core (Colvin, 1986; Manson, 1995; Gouzoules & Gouzoules, 1987). This is fairly similar to the social arrangements of ring-tailed lemurs, certainly much more so than the social structure of any of the apes, and so this seemed a good place to begin. Weiss, Adams, Widdig, and Gerald (2011) found six personality traits in rhesus macaques, these being Confidence, Openness, Dominance, Friendliness, Activity, and Anxiety. For the HPQ to be appropriate for use on rhesus macaques, several minor modifications had to be made from the version suitable for apes. For the most part these changes made no substantive differences, simply exchanging the words "enclosure" for "environment" to reflect the free-ranging nature of the subjects and "chimpanzee" to "monkey" for obvious reasons (Weiss, Adams, Widdig, & Gerald, 2011).

In this study, we seek to modify the HPQ slightly so that it can be applied to ring-tailed lemurs to identify their personality structure. Due to the much

greater differences evolutionarily, ecologically, and behaviourally from the great apes we believe that a greater degree of modification to the questionnaire may be necessary and a thorough investigation into its applicability is warranted in this case.

4.2 Methods

4.2.1 Subjects

The subjects in this study are five male ring-tailed lemurs *Lemur catta* housed together at the Edinburgh Zoo. Three individuals were rated by two different raters while the other two were only rated by one. Both raters were familiar with the individuals for approximately one year after the lemurs had all been transferred to the zoo as a group and replaced the previous group of seven females. In general raters had more than five years experience each working with ring-tailed lemurs.

4.2.2 Measure

The Hominoid Personality Questionnaire (King et al., 2006) consists of 54 adjectives with one to three sentences each explaining the meaning of the adjective and its application in relation to nonhuman personality. An example item is as follows: "AFFECTIONATE: Subject seems to have a warm attachment or closeness with other monkeys. This may entail frequent grooming, touching, embracing, or lying next to others." (For the full questionnaire see Appendix B) Raters are instructed to assess individuals on these adjectives on a seven-point Likert scale from "1. *Displays either total absence or negligible amounts*

of the trait." to "7. *Displays extremely large amounts of the trait.*" Raters are also told to provide an overall subjective impression of an individual's typical behaviour rather than specific instances or frequency counts of behaviour for their ratings.

The specific version of the HPQ used as a basis for this study was the Monkey Personality Trait Assessment adapted from the HPQ by Weiss, Adams, Widdig, and Gerald (2011) for use on rhesus macaques.

4.2.3 Qualitative Assessment

The qualitative portion of the assessment can be divided into several parts. Firstly, an overall survey of the items was conducted by the researchers. The purpose of this was to identify any obvious changes that needed to be made, such as the substitution of the word "monkey" for "lemur" and to note any potentially problematic or ill-suited items. These were defined as any items containing references in their descriptions to behaviours or characteristics that were not appropriate for lemurs, for example references to facial expressions or tool use, or those that lacked certain relevant lemur-specific examples of behaviours such as scent marking. Items were also identified that may not be suited to lemurs due to their relevance or the capacity either for lemurs to express or for raters to be able to accurately assess such behaviours.

After these potentially problematic items were identified, the head caretaker of the subject lemurs was consulted to discuss the relevance and appropriateness of the items from the perspective of the rater and as a person with practical expertise observing lemur behaviour over a long period. Items previously defined as problematic were brought up and any other items they thought inappropriate were also discussed. The caretaker also provided guidance on the

use of specific examples of behaviours used in the questionnaire and provided information on what behaviours commonly observed could be better tools in assessing lemurs on these adjectives.

4.2.4 Quantitative Assessment

Interrater reliability between the two raters in this study was also measured for the three individuals on which multiple ratings had been collected. This was done by using two intraclass correlations $ICC(3,1)$ and $ICC(3,k)$ (Shrout & Fleiss, 1979). For this study a threshold of less than .10 was identified as a potentially problematic score and worthy of further investigation.

4.3 Results

4.3.1 Qualitative Results

First and easiest to modify were the semantic changes. The word "lemur" was substituted in for the word "monkey" wherever it occurred. It was judged that the word "environment" in this case was also appropriate and would not cause confusion so it was not changed back to "enclosure" in this study.

There were also concerns about the item Autistic and the potential therein for mischaracterisation. As this term is primarily used in humans to identify a specific set of pathological conditions (Frith, 2003) and, unlike the items Depressed or Anxious, it does not have a distinct common-usage definition separate from this clinical usage. This clinical use also carries along with it a set of implied characteristics that may be imposed on the rating beyond the clarification given in the item description. As such, and to avoid issues

with misunderstanding of the personality ratings as a diagnosis or as implicit acceptance of the presence of autism-spectrum disorder in nonhumans without proper support, we have judged that it would best serve the interests of accurate measurement to relabel the item as "Stereotypic." The item description remains unchanged, except in this case for relevant behavioural examples, and we hope that this modification will allow for better measurement of this personality construct as intended. Concerning this issue with previous scales, if they were administered properly and the item labels were treated as intended there should be no problem with associations.

In the initial review, several items were identified by the researchers as having the potential to be problematic in their application to lemurs. The items Helpful, Manipulative, and Imitative were singled out as not having a high degree of relevance to the target species due to differences in social behaviour and cognitive ability between ring-tailed lemurs and the other species assessed with this measure. Four items were also identified as being potentially limited in their ability to be assessed by raters in the context of lemurs. These items overlapped with the items previously selected as being inappropriate and added on to this the item Inventive.

In the interview with the primary caregiver for ring-tailed lemurs at the Edinburgh Zoo, several of these same issues were confirmed. There were shared opinions on the lack of relevance and difficulty of application of the four items identified in the initial review and more items were proposed such as Innovative and Sympathetic. The caregiver also raised some general concerns about the applicability of the questionnaire as a whole but accepted that a uniform measure was preferable for comparisons of personality between species. They also raised the issue of identification in this particular instance. Sharing their

experience working with chimpanzees and other primates, the caregiver noted that the ring-tailed lemurs were much more difficult to identify as individuals than other species at a glance (relying on coloured collars and banding for identification) and this may have a limiting effect on the overall sense of behavioural impression that is necessary to complete these ratings.

Several examples in the item descriptions were also put forward as not being useful in the assessment of lemurs on those adjectives. In the item Fearful, the example behaviours were changed from "screaming, grimacing, running away" to "squealing, fleeing the area" to remove references to facial expressions not expressed by ring-tailed lemurs and to better reflect vocalisation and movement patterns. Changes were also made to the item Stereotypic. Again example behaviours were replaced, "rocking" and "self-clasping" are not observed in lemurs with the same frequency as in chimpanzees and these were replaced by the behavioural examples "pacing" and "pulling out hair." An addendum was given to Sociable as well in the form of a qualifying behavioural example "such as grooming." Finally, a sentence was added to the description of the item Submissive: "For example, giving agonistic vocalisations such as yips when approaching another lemur." This is in reference to dominance-related vocalisations observed in ring-tailed lemurs (Bolt, 2013).

While olfactory signalling plays a large part in communication between lemurs, it was judged by both researchers and caretakers that to modify any of the existing items to incorporate this, such as incorporating chemical analysis from scent marking, would be to change their meaning substantively. It was decided that greater value lay in maintaining the integrity of the scale than in changing or adding items to incorporate species-specific communication methods and that the underlying concepts, particularly with the instruction to raters

not to rely on frequency or specific instances or behaviours but rather overall impressions, too much of the universal applicability of the questionnaire would be lost.

4.3.2 Quantitative Results

In the reliability analysis of these items, twenty-five were identified as being below the threshold of reliability (Tables 4.1 & 4.2). These items were Fearful, Stereotypic, Curious, Reckless, Sympathetic, Innovative, Helpful, Manipulative, Gentle, Impulsive, Dependent, Irritable, Unperceptive, Decisive, Depressed, Conventional, Defiant, Intelligent, Protective, Clumsy, Erratic, Anxious, Lazy, Unemotional, and Imitative. Though Quitting and Inventive were the only two items with significant correlations, the severe limitations on the number of subjects calls their true reliability into question.

4.4 Discussion

Overall, the raters were able to provide ratings on ring-tailed lemurs using this questionnaire with relatively little difficulty. Several changes were made between the initial questionnaire and the version used to collect data in this study and all appeared to have improved or otherwise facilitated the collection of data. The early semantic changes were fairly self-evident and required little deliberation over their implementation. The same goes for the changes to several examples throughout the questionnaire to be more relevant to lemurs specifically. These changes were supported and informed by the interviewed lemur caretaker and several examples were provided or amended by them to better encapsulate the behaviours described.

Table 4.1: Lemur Personality Questionnaire Intraclass Correlations

Item	ICC3	F	p
Fearful	0.00	1.0	.50
Dominant	0.77	7.8	.11
Persistent	0.20	1.5	.40
Cautious	0.14	1.3	.43
Stable	0.08	1.2	.46
Stereotypic	0.00	1.0	.50
Curious	0.00	1.0	.50
Thoughtless	0.20	1.5	.40
Stingy	0.58	3.8	.21
Jealous	0.80	9.0	.10
Individualistic	0.14	1.3	.43
Reckless	0.00	1.0	.50
Sociable	0.83	11.0	.09
Distractible	0.20	1.5	.40
Timid	0.00	1.0	.50
Sympathetic	0.00	1.0	.50
Playful	0.20	1.5	.40
Solitary	0.70	5.6	.15
Vulnerable	0.44	2.6	.28
Innovative	0.00	1.0	.50
Active	0.73	6.5	.13
Helpful	0.00	1.0	.50
Bullying	0.40	2.3	.30
Aggressive	0.73	6.5	.13
Manipulative	0.00	1.0	.50
Gentle	0.01	1.2	.46
Affectionate	0.64	4.5	.18

Table 4.2: Lemur Personality Questionnaire Intraclass Correlations

Item	ICC3	F	p
Excitable	0.73	6.5	.13
Impulsive	0.00	1.0	.50
Inquisitive	0.60	4.0	.20
Submissive	0.52	3.2	.24
Cool	0.14	1.3	.43
Dependent	0.00	1.0	.50
Irritable	0.00	1.0	.50
Unperceptive	0.00	1.0	.50
Predictable	0.75	7.0	.13
Decisive	0.00	1.0	.50
Depressed	0.00	1.0	.50
Conventional	0.00	1.0	.50
Sensitive	0.20	1.5	.40
Defiant	0.00	1.0	.50
Intelligent	0.00	1.0	.50
Protective	0.00	1.0	.50
Quitting	1.0	*N/A*	.00
Inventive	1.0	*N/A*	.00
Clumsy	0.00	1.0	.50
Erratic	0.00	1.0	.50
Friendly	0.40	2.3	.30
Anxious	0.00	1.0	.50
Lazy	0.00	1.0	.50
Disorganized	0.17	1.4	.42
Unemotional	0.00	1.0	.50
Imitative	0.00	1.0	.50
Independent	0.37	2.2	.32

The four items, Imitative, Helpful, Manipulative, and Inventive that were identified as potentially problematic at the beginning of the study were also amongst those selected by the lemur caretaker at the zoo as being difficult to assess in lemurs. There was agreement on the limited applicability of these items in lemurs compared to chimpanzees or humans. Lemurs tend to show much less cooperative or imitative behaviour and do not appear to possess a theory of mind in the same sense that humans or chimpanzees do (Premack & Woodruff, 1978; Call & Tomasello, 2008). Even rhesus macaques, to whom the HPQ was successfully applied substantively unchanged, show a greater capacity for understanding the capacity for independent thought and knowledge in others than do lemurs (Anderson & Mitchell, 1999). As such, the items related to this area, particularly Manipulative and Imitative, may not be useful when applied to lemurs. The item Inventive may also have limited utility when compared to ratings of apes and other monkeys because the lower cognitive capacity in lemurs may not allow for as wide or as obvious of an expression of this characteristic and therefore it may be difficult to be reliably assessed by raters (Sandel, MacLean, & Hare, 2011) , though evidence does exist of relatively higher social cognitive ability than nonsocial in ring-tailed lemurs (MacLean et al., 2013). It is encouraging that these issues were identified independently by the caretaker who was very familiar with the behaviour of ring-tailed lemurs and the practicality of these items may be a point of concern for future studies.

The change in the label of the item Autistic to Stereotypic is also a positive step in the field of personality in nonhuman primates. In measuring personality in item-rating based questionnaires, it is generally seen as an advantage if items are unambiguous and specific to the construct they are attempting to measure (Angleitner, John, & Löhr, 1986). It follows then that if we are able

to clarify the items in our questionnaires and remove some of this ambiguity and outside connotations that by doing so we will improve our scale. In this particular instance, we are also treading the line of highly complex clinical definitions and diagnoses in our choice of words. By using a word like autistic as a personality item, we run the risk of accidentally associating our personality dimensions with clinical conditions that may not be present in the species we are studying (Amaral, Bauman, & Mills Schumann, 2003). There are also several important social aspects to the connotations of terms such as these that must be taken into account. Most of the ratings on questionnaires such as these come from zookeepers and animal caretaker, the majority of whom do not have a background in psychology (e.g. King & Figueredo, 1997; Weiss et al., 2009, 2015). As such, they may be less likely to remove the lay interpretations of clinical terms from the specific context of personality item ratings and this may cause confusion in the ratings depending on differing levels of familiarity with autism spectrum disorder. There is also the risk of misinterpretation by the wider public, either accidentally by those looking for fundamental understanding of disorders or deliberately by those who would seek to classify people with disabilities as "animals." In the end, the best course of action for us as personality researchers is to relabel items such as Autistic and move away from the use of terms from tangentially related literature into a new and often tenuously related context.

The quantitative analysis, given the fact that only three individuals could be compared between two raters, was less of a specific source of information and more of a broad interpretation of the reliabilities. The fact that nearly half of the items were unreliable was most likely a result of the small sample size and must be interpreted with this in mind. What was notable in this

was that all of the items identified by researchers and caretakers were in the unreliable category and none were considered reliable but this is also possibly coincidence. With only five individuals, it would be fruitless to attempt to analyse the factor structure of personality in ring-tailed lemurs and so this is left to future research.

4.4.1 Recommendations for Changes in the HPQ

When continuing the trend of applying the HPQ to an ever-broadening collection of species, we have several recommendations for ensuring that personality is measured in the most useful and effective way possible. The first principle of application should be to do nothing. In an ideal world, the same questionnaire would be able to be used to measure personality in any species one would care to choose and the resulting personality trait structures would be directly comparable. This is not the case however, and in fact many differences between species that make them interesting subjects of personality research are the very things hindering the application of this questionnaire and so some adaptations have to be made (S. D. Gosling, 2001; King & Weiss, 2011; Weiss, 2018). However, to preserve to the greatest degree the comparative psychological value of these trait structures, best practice would dictate that the minimum necessary changes to the scale be made.

An alternative to this path exists in the development of a new, more universal questionnaire. Just as the CPQ was adapted into the OPQ and then the HPQ, there is the possibility for more items to be added to increase the representation of undervalued traits in the measure to work towards a sort of Universal Questionnaire of Everything that could be applied to all species. While these expansions are theoretical at this point, it is certainly within the

realm of future work to develop ever more universal personality questionnaires.

The second recommendation of the application of the HPQ to new species that has become apparent in this study is that, when modifications are unavoidable, they should focus on changing examples and descriptive semantics while avoiding changing the construct measured. This follows the same principle of conservation of comparative value as the first tenet while admitting that some behaviours are not one-size-fits-all. In fact is may be more beneficial in the future to make modifications away from specific examples altogether if possible, using instead broad characterisation to avoid similar situations repeating themselves for every new species application.

The third recommendation drawn out from this study is to take steps to move away from ambiguous or homonymous labels with relevance in connected fields. While in some instances the reuse of terms can aid in our comparative research such as the use of the same labels for five personality factors in both humans and chimpanzees(King et al., 2005), for the most part they only serve to sow confusion. One deeply entrenched example of this is the personality trait label "dominance" which is applied to a number of species (e.g. King & Figueredo, 1997; Weiss, Adams, Widdig, & Gerald, 2011; Morton et al., 2013). It being closely associated with the separate construct of social dominance does not do any favours for anyone when discussing the two together. In this study we focused on one item in particular that exhibits these and other problems, Autistic. While here renaming the item Stereotypic seems to have addressed some of the concerns illustrated above, the potential for this confusion also exists in other items with co-opted terms from clinical research like Depressed and Anxious. It is a point for future studies to review and assess whether the field would benefit from changes such as this.

4.4.2 Future Research

On the topic of continuing research, the most obvious path is to apply this questionnaire to a large sample of ring-tailed lemurs to build up a sufficient dataset to determine the factor structure of their personality. While the tools are all present and contained in this study, the limiting factor is data collection and so this should be an easy step to take in advancing the field. After this structure has been determined, there is a deep well of confirmatory work that can be done looking at the hierarchical levels of ring-tailed lemur personality (see Chapters 2 & 3) as well as further data collection to branch out to wild individuals, longitudinal studies, and also research on behavioural correlates or predictors of personality in these lemurs.

Another almost self-evident next step in the research is to try and expand outwards to other species of lemurs or to lorises. While the most prominent obstacle here is again the practicalities of data collection, it is worth noting that many other species of lemur and also lorises do not live in large social groups and so new problems may arise in the application of a questionnaire that relies partly on questions related to social interactions. One place to start might be the sifaka in the lemur family *Indriidae*. These lemurs also live in social groups of around 13 individuals and this social complexity may facilitate personality study (Pochron, Tucker, & Wright, 2004).

Further research on ring-tailed lemurs could also follow in the footsteps of human and ape personality research by looking at predictors of health, welfare, and well-being (e.g. Weiss et al., 2009; Herrelko et al., 2012; Altschul et al., 2018). It would also be beneficial to look at these predictors on the level of items or nuances (McCrae, 2015) as they could provide a more specific correlation with greater predictive utility than the dimensions as a whole (Mõttus et al.,

2017, 2018).

In conclusion, this study lays the groundwork for the expansion of personality research into new and uncharted territories. Specifically, those territories lying across the Mozambique Channel crossed so many millions of years ago by the early *Lemuriformes*.

Chapter 5

Conclusion

5.0.1 Chapter Summaries

Chapter 1 In this published book chapter, we explore the evolutionary history of the development of personality with age. Personality has developed in living animals over millions of years to play an adaptive role in evolution, presenting as multiple structures in different species depending on the selective pressures relevant to those species. Drawing from MacArthur and Wilson's (1963) life history theory and the idea of balancing selection (D. M. Buss, 2009) we suggest that certain consistent behavioural variations led to greater reproductive success and were therefore preserved as personality traits. Where different strategies were available resulting in comparable levels of success, variations in these behaviours occurred leading to individuals favouring one strategy over another. Trade-offs in the advantages conveyed by different levels of personality traits being conserved and further specialisation based on the specific demands of the species such as complex social structures. By comparing personality development across the lifespan in different species, we can begin to explore the utility of these specific traits in relation to developmental

influences, though here seemingly not related to merely social roles as defined in humans, and thus identify common developmental arcs in personality among species.

Chapter 2 Looking at the overall results from Chapter 2, we can see that there are clear facets present in the personality structure of nonhuman apes. While several of these facets contain multiple items they are, for the most part, representative of only one item. Interestingly there are several consistent groupings of items that exist between species and several that diverge in certain species and, by extension, perhaps under certain circumstances in ecology or social structure. An example of a facet combination that is fairly consistent throughout are the items Sociable and Friendly. In every species studied except for bonobos, these two items group together in a facet under extraversion or sociability in the case of gorillas. On the other side of the coin, when we look at the item Intelligent we see that it is always represented by a single-item facet regardless of the species or factor under which it is organised. Consistencies such as these suggest deeper relationships in the connection of these items in the evolutionary development in personality and it would be very interesting indeed to see how these items would be connected or not connected in other species with greater evolutionary distances and more varied social structures such as lemurs or elephants.

The fact that so many of these facets only represent one item may be a result of the specificity of the items and the limited size of these questionnaires compared to the human measures, often containing five times the number of items or more (McCrae & Costa, 2010). Due to this lack of item interrelation, facets may not be the most useful tool for conceptualisation or usefulness of

lower-order hierarchy in personality in these species and using these shorter questionnaires.

Chapter 3 More useful, it would seem, are the still-lower levels of hierarchy in the item or nuance level. In our examination of these in Chapter 3 we can see that in the context of age-related changes in personality some changes occur at the factor level and some at the item level. Factors such as extraversion as seen in orangutans and openness in chimpanzees and bonobos are strongly driven at the factor level with every item loading onto the factor significantly varying with age. Other factors have significant variation with age at the factor level but on closer investigation show this change is driven by only a few items. Still others show the inverse, with the factor level differences failing to reach significance but certain items contained within changing with age. In these cases a large amount of detail about the variation is lost when only considering the factor level and clear benefits can be taken from this expanded analysis. These correlations with age are indicative of the potential for much more refined investigations into personality correlates in nonhuman animals and this study acts as the introduction of the application personality nuances to the field of nonhuman personality. In future work these specific predictors may be incredibly useful when looking for specific drivers in personality of outcomes, similar to those described by Mõttus et al. (2017). In terms of comparative analysis, using nuances similarly allows for a detail in comparison that can potentially highlight specific driving forces in trait differentiation and allow for investigation into the specific external evolutionary pressures that are driving these differences.

Also noted by Mõttus et al. (2017) are the criteria for validation of these

nuances as they were used in humans. Specifically, these are corroborations from multiple measures' stability over time, and the genetic foundation of this level of the hierarchy. All of these are exciting new areas of future study that stem from the work included here. An investigation of multi-method approaches may need to be be slightly more creative than the same validation in humans as here we lose out on the most commonly used and easiest to collect personality measure, the self-report questionnaire. Instead, future research will have to rely on other instruments like independent questionnaires like the ones created by Stevenson-Hinde and Zunz (1978) or Dutton et al. (1997) to measure personality in rhesus macaques or on behavioural measures of personality. These have been used extensively before the development of these questionnaires across a wide range of species (S. D. Gosling & John, 1999) and, while time consuming and sometimes difficult to administer, may be the most thorough cross-method tool available to us. The issue of stability over time is a relatively easy one to address where the only further requirement is the collection of another round of personality data on the same individuals to compare against the data included in this study. In this way we should get a very clear picture of hopefully the necessary rank-order stability with the same scale of data collected and see which of these items are stable over long periods of time. While questions of stability have been addressed in a cross-sectional way (Weiss & King, 2015) and using other measures (Weiss, Gartner, Gold, & Stoinski, 2013), a new round of data collection using the same questionnaire for these species would be incredibly valuable to not just the investigation of nuances but to the field as a whole. The familiar refrain of more data holds true in the case of the genetic foundation of this level of personality as well. Here however it is data on the pedigree and relatedness of these animals that

may help us establish genetic influence (Weiss et al., 2000; Adams et al., 2012) and fulfil the third confirmatory criterion of Mõttus et al. (2017).

Chapter 4 While an increase in depth of knowledge in the form of increased understanding and application of the lower orders of the personality hierarchical structure in nonhuman primates is highly valuable to the field, so too is the branching out that is the expanded application of personality questionnaires to new species. In this case, we have established guidelines and laid the foundation for an expansion of personality research to one of the most distant primate relatives to humans, the ring-tailed lemur. While ideally the same questionnaire would be applied to all species, primate or otherwise, without any loss of relevance or utility, due to the often numerous and dramatic differences between species there are often several items that are not relevant and may be difficult to apply conceptually to the target species. Here we have identified using qualitative measures some of these potentially problematic items and recommend they be given special attention in further expanded data collection. Examples and semantic changes are also often necessary until items and descriptions can be created that are universally applicable, we have highlighted changes here that make the HPQ more suitable for use on ring-tailed lemurs. Another point that we have noted here is the issues surround descriptive adjectives with additional meanings, particularly those with clinical psychological definitions. Here we recommend changing the item Autistic in the HPQ to another similar term Stereotypic with the same defining sentences. The purpose of this it to reduce ambiguity in the meaning of our personality items and to separate the measures of personality used here from any implications of clinical diagnoses or applications. We are also concerned with some of the social issues

surrounding terms such as these and seek to avoid any potential issues in their use by modifying our items to something with an equivalent meaning but free from the other semantic popular associations.

5.0.2 Final Conclusions

When taken as a whole, the work contained herein accomplishes two main goals. First, we have contributed greatly to the knowledge of the hierarchical structure of personality in nonhuman great apes. While the lower-order structure of personality in humans has been clearly defined and researched in depth for several decades, at this point it has not been expanded to this degree in nonhuman apes. Here we have provided clear identifications of the facet structure from a statistically-driven standpoint for chimpanzees, orangutans, bonobos, and gorillas. Not limited to the facet level, we have also investigated the developmental trajectories of personality nuances in these four great apes. Previously only studied at a factor level or in a limited number of imposed facets derived from human facets, we have shown the full detailed complement of item associations with age in these species. This analysis has revealed that, while some factors show corresponding changes in all items that comprise them, in most cases these trends are driven by changes in specific items. Some of these changes are quite dramatic and both items and the facets identified in this thesis have enormous potential for the refining of personality as an associative or predictive measure of other outcomes or traits. Both of these studies make use of what is, to date, the largest collection of personality questionnaire data from the HPQ and its predecessors ever assembled for one body of work. It is our hope that continued use can be made of these datasets and these tools we have created can be used to further the field of nonhuman personality

research.

This leads directly to the second major accomplishment of this thesis which is the creation of a number of valuable springboards for the rapid advancement of knowledge. Both the application of personality facets and nuances to nonhuman personality has great potential for use in further research limited only by will and imagination. These can be applied to almost any other correlational study using personality to allow for a higher level of detail and the potential for more specific associations with greater utility using these lower hierarchical levels. Two obvious next steps for this is a re-examination of personality correlates with welfare and subjective well-being in these apes. Both are important issues in animal care and management with established personality correlates and the increased strength and specificity of some of these item or facet association can allow for better prediction of issues in these areas and have great potential for application in zoos and sanctuaries in particular. There is also the options available for expansions of breadth in the field as well as increased depth in understanding and practice. Specifically, these ideas can be easily spread to personality study of other species using the same questionnaires both primate and otherwise. One in particular also set up here is the identification of personality structure in ring-tailed lemurs. We have shown that it is possible to use the HPQ in this species with only minor modifications and the combination of facet and nuance analysis allows for clear and thorough research to be conducted on these lemurs using the tools set up in this body of work.

In closing, the establishment of more principles and ideas utilised in human personality research can dramatically strengthen our understanding of personality in our evolutionary relatives and by extension our common ancestors. Using facets and nuances in these species also has a number of practical ap-

plications when applied to personality correlates such as welfare or well-being and have the potential to be great tools in the care and maintenance of these species. We sincerely hope that this work will be taken up in the toolkit of personality researchers working with nonhuman animals and that their potential value to the greater body of research is realised.

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Appendix A

Hominoid Personality Questionnaire

CHIMPANZEE PERSONALITY TRAIT ASSESSMENT

Chimpanzee personality assessments can be made with this questionnaire by assigning a numerical score for all of the personality traits listed on the following pages. Make your judgments on the basis of your own understanding of the trait guided by the short clarifying definition following each trait. The chimpanzee's own behaviors and interactions with other chimpanzees should be the basis for your numerical ratings. Use your own subjective judgment of typical chimpanzee behavior to decide if the chimpanzee you are scoring is above, below, or average for a trait. The following seven point scale should be used to make your ratings.

1. **Displays either total absence or negligible amounts of the trait.**
2. **Displays small amounts of the trait on infrequent occasions.**
3. **Displays somewhat less than average amounts of the trait.**
4. **Displays about average amounts of the trait.**
5. **Displays somewhat greater than average amounts of the trait.**
6. **Displays considerable amounts of the trait on frequent occasions.**
7. **Displays extremely large amounts of the trait.**

Please give a rating for each trait even if your judgment seems to be based on a purely subjective impression of the chimpanzee and you are somewhat unsure about it. Indicate your rating by placing a cross in the box underneath the chosen number. $\boxed{\times}$

Finally, do not discuss your rating of any particular chimpanzee with anyone else. As explained in the handout accompanying this questionnaire, this restriction is necessary in order to obtain valid reliability coefficients for the traits.

CHIMPANZEE PERSONALITY TRAIT ASSESSMENT

Chimpanzee's full name:_____

Rater's full name:_____

Date (Mon/Day/Yr):_____

FEARFUL: Subject reacts excessively to real or imagined threats by displaying behaviors such as screaming, grimacing, running away or other signs of anxiety or distress.

least most

1	2	3	4	5	6	7
☐	☐	☐	☐	☐	☐	☐

DOMINANT: Subject is able to displace, threaten, or take food from other chimpanzees. Or subject may express high status by decisively intervening in social interactions.

least most

1	2	3	4	5	6	7
☐	☐	☐	☐	☐	☐	☐

PERSISTENT: Subject tends to continue in a course of action, task, or strategy for a long time or continues despite opposition from other chimpanzees.

least most

1	2	3	4	5	6	7
☐	☐	☐	☐	☐	☐	☐

CAUTIOUS: Subject often seems attentive to possible harm or danger from its actions. Subject avoids risky behaviors.

least most

1	2	3	4	5	6	7
☐	☐	☐	☐	☐	☐	☐

STABLE: Subject reacts to its environment including the behavior of other chimpanzees in a calm, equable, way. Subject is not easily upset by the behaviors of other chimpanzees.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

AUTISTIC: Subject often displays repeated, continuous, and stereotyped behaviors such as rocking or self clasping.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

CURIOUS: Subject has a desire to see or know about objects, devices, or other chimpanzees. This includes a desire to know about the affairs of other chimpanzees that do not directly concern the subject.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

THOUGHTLESS: Subject often behaves in a way that seems imprudent or forgetful.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

STINGY/GREEDY: Subject is excessively desirous or covetous of food, favored locations, or other resources in the enclosure. Subject is unwilling to share these resources with others.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

JEALOUS: Subject is often troubled by others who are in a desirable or advantageous situation such as having food, a choice location, or access to social groups. Subject may attempt to disrupt activities of advantaged chimpanzees.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

INDIVIDUALISTIC: Subject's behavior stands out compared to that of the other individuals in the group. This does not mean that it does not fit or is incompatible with the group.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

RECKLESS: Subject is rash or unconcerned about the consequences of its behaviors.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

SOCIABLE: Subject seeks and enjoys the company of other chimpanzees and engages in amicable, affable, interactions with them.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

DISTRACTIBLE: Subject is easily distracted and has a short attention span.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

TIMID: Subject lacks self confidence, is easily alarmed and is hesitant to venture into new social or non-social situations.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

SYMPATHETIC: Subject seems to be considerate and kind towards others as if sharing their feelings or trying to provide reassurance.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

PLAYFUL: Subject is eager to engage in lively, vigorous, sportive, or acrobatic behaviors with or without other chimpanzees.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

SOLITARY: Subject prefers to spend considerable time alone not seeking or avoiding contact with other chimpanzees.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

VULNERABLE: Subject is prone to be physically or emotionally hurt as a result of dominance displays, highly assertive behavior, aggression, or attack by another chimpanzee.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

INNOVATIVE: Subject engages in new or different behaviors that may involve the use of objects or materials or ways of interacting with others.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

ACTIVE: Subject spends little time idle and seems motivated to spend considerable time either moving around or engaging in some overt, energetic behavior.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

HELPFUL: Subject is willing to assist, accommodate, or cooperate with other chimpanzees.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

BULLYING: Subject is overbearing and intimidating towards younger or lower ranking chimpanzees.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

AGGRESSIVE: Subject often initiates fights or other menacing and agonistic encounters with other chimpanzees.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

MANIPULATIVE: Subject is adept at forming social relationships for its own advantage, especially using alliances and friendships to increase its social standing. Chimpanzee seems able and willing to use others.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

GENTLE: Subject responds to others in an easy-going, kind, and considerate manner. Subject is not rough or threatening.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

AFFECTIONATE: Subject seems to have a warm attachment or closeness with other chimpanzees. This may entail frequently grooming, touching, embracing, or lying next to others.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

EXCITABLE: Subject is easily aroused to an emotional state. Subject becomes highly aroused by situations that would cause less arousal in most chimpanzees.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

IMPULSIVE: Subject 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.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

INQUISITIVE: Subject seems drawn to new situations, objects, or animals. Subject behaves as if it wishes to learn more about other chimpanzees, objects, or persons within its view.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

SUBMISSIVE: Subject often gives in or yields to another chimpanzee. Subject acts as if it is subordinate or of lower rank than other chimpanzees.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

COOL: Subject seems unaffected by emotions and is usually undisturbed, assured, and calm.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

DEPENDENT/FOLLOWER: Subject often relies on other chimpanzees for leadership, reassurance, touching, embracing and other forms of social support.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

IRRITABLE: Subject often seems in a bad mood or is impatient and easily provoked to anger exasperation and consequent agonistic behavior.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

UNPERCEPTIVE: Subject is slow to respond or understand moods, dispositions, or behaviors of others.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

PREDICTABLE: Subject's behavior is consistent and steady over extended periods of time. Subject does little that is unexpected or deviates from its usual behavioral routine.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

DECISIVE: Subject is deliberate, determined, and purposeful in its activities.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

DEPRESSED: Subject does not seek out social interactions with others and often fails to respond to social interactions of other chimpanzees. Subject often appears isolated, withdrawn, sullen, brooding, and has reduced activity.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

CONVENTIONAL: Subject seems to lack spontaneity or originality. Subject behaves in a consistent manner from day to day and stays well within the social rules of the group.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

SENSITIVE: Subject is able to understand or read the mood, disposition, feelings, or intentions of other chimpanzees often on the basis of subtle, minimal cues.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

DEFIANT: Subject is assertive or contentious in a way inconsistent with the usual dominance order. Subject maintains these actions despite unfavorable consequences or threats from others.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

INTELLIGENT: Subject is quick and accurate in judging and comprehending both social and non-social situations. Subject is perceptive and discerning about social relationships.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

PROTECTIVE: Subject shows concern for other chimpanzees and often intervenes to prevent harm or annoyance from coming to them.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

QUITTING: Subject readily stops or gives up activities that have recently been started.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

INVENTIVE: Subject is more likely than others to do new things including novel social or non-social behaviors. Novel behavior may also include new ways of using devices or materials.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

CLUMSY: Subject is relatively awkward or uncoordinated during movements including but not limited to walking, acrobatics, and play.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

ERRATIC: Subject is inconsistent, indefinite, and widely varying in its behavior and moods.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

FRIENDLY: Subject often seeks out contact with other chimpanzees for amiable, genial activities. Subject infrequently initiates hostile behaviors towards other chimpanzees.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

ANXIOUS: Subject often seems distressed, troubled, or is in a state of uncertainty.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

LAZY: Subject is relatively inactive, indolent, or slow moving and avoids energetic activities.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

DISORGANIZED: Subject is scatterbrained, sloppy, or haphazard in its behavior as if not following a consistent goal.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

UNEMOTIONAL: Subject is relatively placid and unlikely to become aroused, upset, happy, or sad.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

IMITATIVE: Subject often mimics, or copies behaviors that it has observed in other chimpanzees.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

INDEPENDENT: Subject is individualistic and determines its own course of action without control or interference from other chimpanzees.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

Appendix B

Lemur Personality Questionnaire

LEMUR PERSONALITY TRAIT ASSESSMENT

Lemur personality assessments can be made with this questionnaire by assigning a numerical score for all of the personality traits listed on the following pages. Make your judgments on the basis of your own understanding of the trait guided by the short clarifying definition following each trait. The lemur's own behaviors and interactions with other monkeys should be the basis for your numerical ratings. Use your own subjective judgment of typical monkey behavior to decide if the lemur you are scoring is above, below, or average for a trait. The following seven point scale should be used to make your ratings.

1. **Displays either total absence or negligible amounts of the trait.**
2. **Displays small amounts of the trait on infrequent occasions.**
3. **Displays somewhat less than average amounts of the trait.**
4. **Displays about average amounts of the trait.**
5. **Displays somewhat greater than average amounts of the trait.**
6. **Displays considerable amounts of the trait on frequent occasions.**
7. **Displays extremely large amounts of the trait.**

Please give a rating for each trait even if your judgment seems to be based on a purely subjective impression of the lemur and you are somewhat unsure about it. Indicate your rating by placing a cross in the box underneath the chosen number. $\boxed{\times}$

Finally, do not discuss your rating of any particular lemur with anyone else. As explained in the handout accompanying this questionnaire, this restriction is necessary in order to obtain valid reliability coefficients for the traits.

LEMUR PERSONALITY TRAIT ASSESSMENT

Lemur's full name:_____

Rater's full name:_____

Date (Mon/Day/Yr):_____

FEARFUL: Subject reacts excessively to real or imagined threats by displaying behaviors such as squealing, fleeing the area, or other signs of anxiety or distress.

least most

1	2	3	4	5	6	7
☐	☐	☐	☐	☐	☐	☐

DOMINANT: Subject is able to displace, threaten, or take food from other lemurs. Or subject may express high status by decisively intervening in social interactions.

least most

1	2	3	4	5	6	7
☐	☐	☐	☐	☐	☐	☐

PERSISTENT: Subject tends to continue in a course of action, task, or strategy for a long time or continues despite opposition from other lemurs.

least most

1	2	3	4	5	6	7
☐	☐	☐	☐	☐	☐	☐

CAUTIOUS: Subject often seems attentive to possible harm or danger from its actions. Subject avoids risky behaviors.

least most

1	2	3	4	5	6	7
☐	☐	☐	☐	☐	☐	☐

STABLE: Subject reacts to its environment including the behavior of otherlemurs in a calm, equable, way. Subject is not easily upset by the behaviors of other lemurs.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

STEREOTYPIC: Subject often displays repeated, continuous, and stereotyped behaviors such as pacing or pulling out hair.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

CURIOUS: Subject has a desire to see or know about objects, devices, or other lemurs. This includes a desire to know about the affairs of other lemurs that do not directly concern the subject.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

THOUGHTLESS: Subject often behaves in a way that seems imprudent or forgetful.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

STINGY/GREEDY: Subject is excessively desirous or covetous of food, favored locations, or other resources in the enclosure. Subject is unwilling to share these resources with others.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

JEALOUS: Subject is often troubled by others who are in a desirable or advantageous situation such as having food, a choice location, or access to social groups. Subject may attempt to disrupt activities of advantaged lemurs.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

INDIVIDUALISTIC: Subject's behavior stands out compared to that of the other individuals in the group. This does not mean that it does not fit or is incompatible with the group.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

RECKLESS: Subject is rash or unconcerned about the consequences of its behaviors.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

SOCIABLE: Subject seeks and enjoys the company of other lemurs and engages in amicable, affable, interactions with them such as grooming.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

DISTRACTIBLE: Subject is easily distracted and has a short attention span.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

TIMID: Subject lacks self confidence, is easily alarmed and is hesitant to venture into new social or non-social situations.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

SYMPATHETIC: Subject seems to be considerate and kind towards others as if sharing their feelings or trying to provide reassurance.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

PLAYFUL: Subject is eager to engage in lively, vigorous, sportive, or acrobatic behaviors with or without other lemurs.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

SOLITARY: Subject prefers to spend considerable time alone not seeking or avoiding contact with other lemurs.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

VULNERABLE: Subject is prone to be physically or emotionally hurt as a result of dominance displays, highly assertive behavior, aggression, or attack by another lemur.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

INNOVATIVE: Subject engages in new or different behaviors that may involve the use of objects or materials or ways of interacting with others.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

ACTIVE: Subject spends little time idle and seems motivated to spend considerable time either moving around or engaging in some overt, energetic behavior.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

HELPFUL: Subject is willing to assist, accommodate, or cooperate with other lemurs.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

BULLYING: Subject is overbearing and intimidating towards younger or lower ranking lemurs.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

AGGRESSIVE: Subject often initiates fights or other menacing and agonistic encounters with other lemurs.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

MANIPULATIVE: Subject is adept at forming social relationships for its own advantage, especially using alliances and friendships to increase its social standing. Lemur seems able and willing to use others.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

GENTLE: Subject responds to others in an easy-going, kind, and considerate manner. Subject is not rough or threatening.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

AFFECTIONATE: Subject seems to have a warm attachment or closeness with other lemurs. This may entail frequently grooming, touching, embracing, or lying next to others.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

EXCITABLE: Subject is easily aroused to an emotional state. Subject becomes highly aroused by situations that would cause less arousal in most lemurs.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

IMPULSIVE: Subject 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.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

INQUISITIVE: Subject seems drawn to new situations, objects, or animals. Subject behaves as if it wishes to learn more about other lemurs, objects, or persons within its view.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

SUBMISSIVE: Subject often gives in or yields to another lemur. For example, giving agonistic vocalisations such as yips when approaching another lemur. Subject acts as if it is subordinate or of lower rank than other lemurs.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

COOL: Subject seems unaffected by emotions and is usually undisturbed, assured, and calm.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

DEPENDENT/FOLLOWER: Subject often relies on other lemurs for leadership, reassurance, touching, embracing and other forms of social support.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

IRRITABLE: Subject often seems in a bad mood or is impatient and easily provoked to anger exasperation and consequent agonistic behavior.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

UNPERCEPTIVE: Subject is slow to respond or understand moods, dispositions, or behaviors of others.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

PREDICTABLE: Subject's behavior is consistent and steady over extended periods of time. Subject does little that is unexpected or deviates from its usual behavioral routine.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

DECISIVE: Subject is deliberate, determined, and purposeful in its activities.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

DEPRESSED: Subject does not seek out social interactions with others and often fails to respond to social interactions of other lemurs. Subject often appears isolated, withdrawn, sullen, brooding, and has reduced activity.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

CONVENTIONAL: Subject seems to lack spontaneity or originality. Subject behaves in a consistent manner from day to day and stays well within the social rules of the group.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

SENSITIVE: Subject is able to understand or read the mood, disposition, feelings, or intentions of other lemurs often on the basis of subtle, minimal cues.

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QUITTING: Subject readily stops or gives up activities that have recently been started.

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1	2	3	4	5	6	7
☐	☐	☐	☐	☐	☐	☐

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☐	☐	☐	☐	☐	☐	☐

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☐	☐	☐	☐	☐	☐	☐

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least most

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☐	☐	☐	☐	☐	☐	☐

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least most

1	2	3	4	5	6	7
☐	☐	☐	☐	☐	☐	☐

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least most

1 2 3 4 5 6 7

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least most

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UNEMOTIONAL: Subject is relatively placid and unlikely to become aroused, upset, happy, or sad.

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1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

IMITATIVE: Subject often mimics, or copies behaviors that it has observed in other lemurs.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐

INDEPENDENT: Subject is individualistic and determines its own course of action without control or interference from other lemurs.

least most

1 2 3 4 5 6 7

☐ ☐ ☐ ☐ ☐ ☐ ☐
