

LOVE, HATRED, AND INDIFFERENCE IN CHIMPANZEES: PERSONALITY,
SUBJECTIVE WELL-BEING (SWB), AND DYADIC-LEVEL BEHAVIOR IN CAPTIVE
CHIMPANZEES (*PAN TROGLODYTES*)

by

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Stephanie M. R. Schneider

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Dedication

To my own personal miracle worker, friend and mentor, Debra Cox-Howard, without whom I would certainly not have been able to overcome my health-related obstacles and return to being a full human being blooming with the entire possibilities of life.

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Love, hatred and indifference in chimpanzees: Personality, Subjective Well-Being, and dyadic-level behavior in captive chimpanzees (*Pan troglodytes*)

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Running head: PERSONALITY, SWB AND DYADIC BEHAVIOR IN CHIMPANZEES

Love, hatred and indifference in chimpanzees: Personality, Subjective Well-Being, and dyadic-level behavior in captive chimpanzees (*Pan troglodytes*)

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Abstract

This dissertation consists of two studies: the first focuses on reliability of chimpanzee personality and subjective well-being (SWB) scores, the second on validating those scores by comparing them to subjective assessments of behavior in dyads. The first measured reliability of scores of personality and subjective well-being (SWB) across ten years. Dominance rank, and the Dominance and Extraversion Factors significantly correlated between time points. In the second study, I investigated the impact of personality, SWB, and demographic characteristics on individual variation in dyadic-level individual behavior. Age predicted likeability in females, and age and rank predicted likeability in males. Neither personality factors nor SWB were correlated to likeability. An Affable domain scale and an Agonistic domain scale were constructed from the personality items. The Affable domain scale correlated with chimpanzees who were scored high neutral in social interactions, and the agonistic scale correlated with low neutral score in social interactions.

Love, hatred and indifference in chimpanzees: Personality, Subjective Well-Being, and dyadic-level behavior in captive chimpanzees (Pan troglodytes): Does something more than rank, age and sex drive the nature of interpersonal relationships in chimpanzees?

Section I: Introduction

Chapter 1. Overview

The reader who is not familiar with the chimpanzee may well be surprised by Kohler's use of the word personality. Indeed, even individuality may cause him to start. But to such incipient skepticism or opposition we would offer the plea that the facts be considered open-mindedly and as nearly as may be in their completeness. Our observations convince us, as do Kohler's, that such terms as temperament, individuality, and personality are as useful, nay even as essential, in the description of chimpanzee as of man.

R. M. and Ada Yerkes, 1929, pg. 129

Personality is defined differently across fields, but the most basic definition found across fields is a pattern, stable across time, of individual variation in responses to one's environment (Dingemanse & Reale, 2005; Gosling & John, 2001; Ijichi, Collins, Creighton, & Elwood, 2013; Kubinyi, Turcsan, & Miklosi, 2009; Reale, Reader, Sol, McDougall, & Dingemanse, 2007; Wolf, van Doorn, Leimar, & Weissing, 2007). In recent years, there has been a surge of research into the structure and nature of personality in non-humans (Brune, Brune-Cohrs, McGrew, & Preuschoft, 2007; Capitano, 2004; Franks et al, 2013; Freeman & Gosling, 2010; Gosling, 2001; Gosling & John, 1999; Menta & Gosling, 2008). A meta-analysis by Gosling and John in 1999 found that personality research had been done in at least 12 non-human species. A more recent survey of the literature by Freeman & Gosling (2010) focused only on non-human primates found 210 research reports on personality in 28 non-human primate species.

Understanding the behavior of non-humans in terms of personality and temperament is not a novel endeavor in the sciences (Darwin, 1872; Freeman & Gosling, 2010; Hebb, 1949;

Kohler, 1927; Menta & Gosling, 2008; Yerkes & Yerkes, 1929). Both Charles Darwin and George Romanes described animal behavior in terms of emotions and personality (Darwin, 1872; Gosling & John, 1999; Hruschka, 2010; Keeley, 2004). However, applying the term personality to non-human animals fell out of favor throughout the rise of behaviorism and the cognitive revolution (Menta & Gosling, 2008). The renewed interest seems to be at least in part a product of increasing interdisciplinary research and the integration of sociobiology into more and more fields.

Non-human personality research is being done by researchers throughout psychology, evolutionary biology, behavioral ecology, zoology, anthropology and beyond to aid in management in captivity (Capitano, 2011; DeCaluwe, Wielebnowski, Howard, Pelican & Ottinger, 2013; Franks, Reiss, Cole, Friedrich & Higgins, 2013; Phillips & Peck, 2007), to better understand other species (Grand, Kuhar, Leighty, Bettinger, Laudenslager, 2012; Horbeck, Miller & Kuczaj, 2013; Konecna, Lhota, Weiss, Urbanek, Adamova, & Pluhacek, 2008; Koski, 2011), and to further our understanding of the evolution of personality across species (Capitano, 2011, 2004; Carere & Maestriperieri, 2008; Freeman & Gosling, 2010; Gosling & John, 1999; Massol & Crochet, 2007; Nave, Sherman, & Funder, 2008; van Oers, 2008; Uher, 2008; Weiss & Adams, 2008; Weiss, Adams, Johnson, 2011; Wemelsfelder, Hunter, Mendl, & Lawrence, 2001; Wolf, van Doorn, Leimer, & Weissing, 2007; Wolf, van Doorn, Leimer, & Weissing, 2007).

The involvement of researchers from so many disciplines as well as the broad range of studies' intended uses (from management concerns to describing the evolution of personality across animal species) have perhaps made it inevitable that at this point the field is impeded by a lack of coherence across disciplines and methodologies (Capitano, 2004; Freeman & Gosling,

2010; Phillips & Peck, 2007; Uher, 2011; Wolf, van Doorn, Leimar, & Weissing, 2007). As yet, there is no common vocabulary or methodological approach across fields (Menta & Gosling, 2008). There are three common means of assessing personality in non-humans: behavioral ethograms/observational studies, impressionistic trait-adjective surveys, and behavioral tests/experiments (Capitanio, 2004; Freeman et al, 2013; Freeman & Gosling, 2010; Gartner & Weiss, 2013; Gosling, 2001; Horback, Miller, & Kuczaj, 2013; Ijichi, Collins, Creighton, & Elwood, 2013; Menta & Gosling, 2008; Mirko, Doka, & Miklosi, 2013; Tetley & O'Hara, 2012; Uher, 2011).

The method employed depends on the field of study, the level of access to subjects, and the goal of the research. **Behavioral ethograms/observational studies** score strictly defined lists of target behaviors during the study period. **Impressionistic trait-adjective studies** ask raters familiar with the subjects to rate each subject on how well a list of adjectives referring to personality or temperament describes each subject. **Behavioral tests/experiments** expose subjects to some novel environmental factor (like a new enrichment tool) or a problem to solve and record individual responses to the test conditions.

Each of these methods has its strengths and weaknesses; however, the potential for growth in non-human personality research seems to be hampered by some mistrust of subjective, impressionistic trait-adjective studies (Uher, 2011). Critics of this method have voiced concerns that the measures are imprecise and vulnerable to anthropomorphic projection (Uher, 2011). Impressionistic trait-adjective studies ask the rater to assess the subject using the rater's informed impression of the subject formed over the entirety of their acquaintance. These assessments can also include items or traits that do not correspond to a quantifiable observed behavior. For example, impressionistic trait-adjective surveys used in previous chimpanzee personality studies

have included items that could not be easily translated into discrete observable behaviors like those used in behavioral ethograms. Examples of such items include: *manipulative*, *decisive*, *independent*, *sympathetic*, *gentle*, and *jealous*. These items that do not have a direct analog in behavioral ethology may be interpreted as sources of imprecision to some critics; but to those who employ impressionistic trait-adjective surveys, these same items demonstrate the strength of this method to compliment and build upon the behavioural ethogram method.

Impressionistic trait-survey methods rely on the ability of human raters to accurately recognize these traits in their non-human subjects by assimilating their experiences with each individual across a variety of contexts and over time to form an impression of the individual. Mistrust of this method was not unfounded during the first, exploratory studies into animal personality; however, there is now a large body of evidence demonstrating the reliability and validity of impressionistic trait-adjective scores in many species (Freeman & Gosling, 2010; Gosling & John, 1999; Mehta & Gosling, 2008; Tetley & O'Hara, 2012).

This dissertation consists of two studies, addressing the reliability and the validity of personality and Subjective Well-Being (SWB) scores collected using impressionistic trait-adjective surveys in captive chimpanzees.

The primary focus of this dissertation is to explore the relationship among personality scores, demographic characteristics, and dyadic-level behavior. I collected data from human raters on personality, SWB, rank and dyad quality in captive chimpanzees.

Study 1: Reliability of personality and SWB scores

Several of the chimpanzees I collected personality and SWB data on were part of a previous research project (Schneider & King, 2008, 2004). This allowed me the opportunity to pursue a second avenue of investigation: to assess the reliability of personality and SWB scores

for this subset of my data across ten years.

Study 2: Validity of personality scores

This study addresses the construct validity of personality scores rated from general, subjective impressions of raters by comparing these scores to a related target behavior also rated from general, subjective impressions: the social behavior of an individual within dyads. Data were collected on captive chimpanzees including: personality and Subjective Well-Being scores, dominance rank, and the affiliative quality of dyadic relationships. The measure of affiliative quality of dyadic relationships is novel to this study. Including the dyadic element of interpersonal relationships in chimpanzees allows this study to establish a research program in non-human interpersonal relationships while also demonstrating the validity of personality scores by predicting a target social behavior.

This study will provide an alternative means to validate impressionistic personality scores by using an analogous, impressionistic measure of a target behavior. This study will be the first to correlate impressionistic trait-adjective scores of personality traits to a behavioral trait also measured by an impressionistic measure. Previous attempts to validate impressionistic scores of personality by correlating them to target behaviors have relied on behavioral ethograms or behavioral tests which produce a score for an individual in that specific context at that one time point (Uher, 2011). In addition to scoring individuals in a very restricted time period and/or context, these other studies are further limited by the choices in their target behavior (Carere & Maestriperi, 2008; Carter, Marshall, Heinsohn, & Cowlshaw, 2012; Franks et al, 2013). As a result, even though these other studies may use similar concepts for their variables, behavioral ethograms or experimental manipulations can actually measure some trait other than the one being measured in the trait-adjective study (Carter, Marshall, Heinsohn, & Cowlshaw, 2012;

Franks et al, 2013).

Chapter 2. The Big Five/Five Factor Model (FFM)

As I have said, finding that something is true of other animals does not prove it true of man; but if there are suggestions of altruism in the dog, and clear evidence of it in larger-brained animals such as chimpanzee and porpoise (Kellogg, 1961; Siebenaler & Caldwell, 1956), it suggests at least that we might look for it in another large-brained animal—man.

D. O. Hebb, 1971, 410

Personality research in non-humans has developed in the presence of the Five Factor Model (FFM), also known as the Big Five, in humans (Brosnan, Newton-Fisher, & van Vugt, 2009; Gosling & John, 1999; Gosling, Rentfrow, & Swann, 2003; Goldberg, 1990; Horback, Miller, & Kuczaj, 2013; MacDonald, 2005; King & Figueredo, 1997; King, Weiss, & Farmer, 2005). The FFM is a widely accepted interpretation of personality structure in humans wherein factor analyses on many data sets have produced five reliably coherent domains of human personality.

The five Factors are Extraversion, Emotionality/Neuroticism, Agreeableness, Conscientiousness, and Openness (Gosling & John, 1999; Gosling, Rentfrow, & Swann, 2003; King & Figueredo, 1997; Piedmont, McCrae, & Costa, 1991). Extraversion includes traits like being outgoing, talkative, bold, uninhibited, and generally friendly (Caspi, Roberts, & Shiner, 2005). Emotionality, once more commonly known as Neuroticism, consists of traits like insecure, jealous, emotional stability/instability, and being worryful (Caspi, Roberts, & Shiner, 2005). Agreeableness refers to being helpful, trusting, and not critical (Caspi, Roberts, & Shiner, 2005). Conscientiousness includes traits like being careful, strong-willed, dependable, and self-reliant (Caspi, Roberts, & Shiner, 2005). Openness refers to one's being open to new experiences and new ideas. In humans, measures of openness often include traits like being curious, imaginative, creative, and spiritual (Caspi, Roberts, & Shiner, 2005). In non-humans, aspects of openness like spirituality or enthusiasm for new experiences are not available without

language. Research incorporating Openness into non-human research has focused on aspects of curiosity, innovativeness, and originality (King & Figueredo, 1997).

The Big Five is not an *a priori*, theoretically driven model, but rather was empirically derived (King & Figueredo, 1997). As early as the late 1800s, the lexical hypothesis emerged that in any naturally evolved language, the vocabulary that results from hundreds of years of daily use will reflect the most relevant and salient characteristics of human nature (King & Figueredo, 1997; McCrae & Costa, 1985). Based on this assertion, surveys were constructed taking terms from the English language related to character and personality. Factor analyses produced the Five Factor Model (McCrae & Costa, 1985). Through many subsequent studies, the FFM has become the most widely accepted model of human personality structure, although certainly not the only one (Gosling & John, 1999).

The Big Five factor structure has emerged with remarkable consistency across studies, methods, and cultures (Heine & Buchtel, 2009; MacDonald, 2005). The first four factors (Extraversion, Emotionality, Agreeableness and Conscientiousness) have shown such consistency cross-culturally (Heine & Buchtel, 2009; King, Weiss, & Farmer, 2005). The final factor, Openness, has shown some variation or flexibility across cultures (Heine & Buchtel, 2009). The research on personality structure in humans has been studied so widely and cross-culturally that it provides an excellent foundation for cross-species comparison.

Impressionistic trait-adjective surveys used in non-human personality research are developed from the same lexical hypothesis as the human scales and were developed in a similar way (King & Figueredo, 1997). A broad range of adjectives are given to raters, along with a short definition, and they are asked to rate the animal subject, rather than themselves or other humans, on that trait (King & Figueredo, 1997). This method has become a common research

tool for non-human personality researchers, just as the survey has become a common tool for those who study human personality. In a review of personality research conducted in captivity since 1995, Tetley & O'Hara (2012) found that out of 30 studies sampled, 80% used impressionistic trait-adjective surveys, 13% used behavioral observations/ethograms, and only 7% used a combination of both methods.

It is especially important that non-human personality researchers should not attempt to replicate the personality structure of humans or any other species. Each new species must be approached with no *a priori* bias as to how many factors may emerge or what those factors may look like. That makes it important to include a wide range of adjective items that reflect each species' behavior and socio-ecological concerns, and to perform factor analyses to extract the personality factor structure of each species (King & Figueredo, 1997).

Anthropomorphic Projection in Non-Human Personality Research

Some critics have suggested that raters were generating personality scores based on their projection of human personality structure onto the apes they are rating (anthropomorphic projection). Weiss, Inoue-Murayama, King, Adams, Matsuzawa (2012) conducted a study demonstrating that raters' scores of chimpanzees and orangutans were not anthropomorphic projections. They collected data on 202 chimpanzees in American zoos, 155 chimpanzees from Japanese research centers, and 174 orangutans from zoos in the U.S., Canada, and Australia (Weiss, Inoue-Murayama, King, Adams, Matsuzawa, 2012). The apes were rated on an impressionistic trait-adjective survey by raters familiar with the subjects (Weiss, Inoue-Murayama, King, Adams, Matsuzawa, 2012).

Two analyses done by Weiss, Inoue-Murayama, King, Adams, Matsuzawa (2012) most clearly address the issue of anthropomorphic projections. The first analysis used an M-Type analysis to adjust a score on an item for a chimp by a rater by subtracting the average score on that item for that rater across all chimpanzee (Weiss, Inoue-Murayama, King, Adams, Matsuzawa, 2012). These adjusted ratings are then used in a Principle Components Analysis. If previous studies using impressionistic trait-adjective survey were tainted by anthropomorphic projection, then the M-type analysis should produce different dimensions: it did not in this study. (Weiss, Inoue-Murayama, King, Adams, Matsuzawa, 2012). The analysis generated six dimensions, four similar to personality dimensions identified in previous research. The other two dimensions were not as similar to the dimensions Neuroticism and Openness but these two domains had fewer items than the other dimensions, so relative lack of similarity to the

personality dimensions could be a product of the small sample size (Weiss, Inoue-Murayama, King, Adams, Matsuzawa, 2012).

The second analysis used was a G-Type analysis. In this analysis the score of an item for an ape by a rater is adjusted by subtracting the average score for the item for that ape across raters (Weiss, Inoue-Murayama, King, Adams, Matsuzawa, 2012). Again, a Principle Components Analysis generated dimensions, but this analysis produces dimensions generated by systematic rater variation not by the chimpanzees' traits (Weiss, Inoue-Murayama, King, Adams, Matsuzawa, 2012). This analysis produced differences in the dimensions produced by Americans rating chimpanzees, Japanese rating chimpanzees, and raters rating orangutans (Weiss, Inoue-Murayama, King, Adams, Matsuzawa, 2012). These results reflect that ratings of ape personality are not anthropomorphic projections, but are scores based on the traits of the apes being rated (Weiss, Inoue-Murayama, King, Adams, Matsuzawa, 2012). This study has answered the primary criticisms raised about impressionistic trait-adjective surveys. As impressionistic, subjective trait-adjective surveys become more widely employed as predictors of potential behavior in captivity, even more studies of reliability and validity of non-human personality will become available.

Chapter 3. Personality in non-human Great Apes

At the same time, the chimpanzee is like man in the complexity of his temperament. If the problem is simpler than with man, it has not been simplified out of existence. As Yerkes has emphasized, there are selfish and generous chimpanzees (perhaps more that are selfish), gluttonous chimpanzees, placid and excitable chimpanzees, trustworthy and untrustworthy, friendly and indifferent and unfriendly, nervous, short-tempered and neurotic chimpanzees—practically all the variety and range of human temperament.

D. O. Hebb, 1949, pg. 193

The recent interest in systematically describing personality in non-humans has revealed some illuminating patterns across species, especially in the great apes. It is natural that, as interest in personality expands beyond our own species, our closest relatives are among the first intensely studied non-humans. Personality in non-humans has perhaps been most systematically studied in our fellow great apes, likely due to their close phylogenetic relationship with our own species that makes them a target for topics of interest in human research. Along with their value as subjects for the benefits in adding to the understanding of human nature, the shared phylogenetic history of all the great apes allows for human raters to apply the mechanisms evolved to understand other humans (such as reading facial expressions and theory of mind) in forming their impressions of apes whose personality characteristics they are asked to rate. This is fortuitous for those of us choosing to study the Great Apes, but it may be less effective in addressing these same concerns in studies of other species, especially as we move beyond the Primate Order.

Personality in great apes

The personality Factor structure of chimpanzees, orangutans, and gorillas had been investigated and published using the impressionistic trait-adjective method (Gold & Maple, 2006; King & Figueredo, 1997; King & Landau, 2003; Weiss, King, & Enns, 2002; Weiss, King & Figueredo, 2000; Weiss, King, & Perkins, 2006). Over all, the studies using the

impressionistic trait-adjective method in the great apes have shown acceptably high inter-rater reliabilities demonstrating that this method can accurately reflect the traits of the subjects being rated (See Koski, 2011; Kuhar, Lukas, & Maple, 2006; Weiss, King & Perkins, 2006; King, Weiss, & Farmer, 2005; Penderson, King, & Landau, 2005; Weiss, King, & Figueiredo, 2000; Lillienfeld, Gershon, Duke, Marino, & de Waal, 1999; King & Figueiredo, 1997; Gold & Maple, 1994, Dutton, 2008). The current study is part of a larger program of research that began with a study of chimpanzees personality (King & Figueiredo, 1997). Since that study of chimpanzee personality, the Great Ape Personality Scale has been applied in some form to wild chimpanzees (Weiss, King, Hopkins, 2007), orangutans (Weiss, King & Perkins, 2006), and gorillas (Eckardt, Steklis, Steklis, et al., 2012).

Orangutan

Weiss, King & Perkins (2006) had raters score 48 items on 152 captive Orangutans using a personality survey form similar to one used in this study and developed from the same earlier form that was used to develop the survey in this study. A Principle Components Factor Analysis of the personality scores showed 5 personality Factors: Extraversion, Dominance, Neuroticism/Emotionality, Agreeableness, and Intellect. The Dominance factor is similar to the one found in chimpanzees (see below). The Intellect factor contained items including intelligent, disorganized and clumsy (Weiss, King, & Perkins, 2006). Extraversion, Emotionality, and Agreeableness were similar domains to those found in all great apes.

Gorilla

Studies of the personality structure of gorillas have been less frequent than those of chimpanzees; however, there have been at least two published studies done using the trait-adjective method in captive gorillas (Kuhar, Stoinski, Lukas, & Maple, 2006; Gold & Maple,

1994). These studies used the Gorilla Behavior Index, a scale similar to, but developed separately from, the Great Ape Personality Survey. These studies identified four personality factors in gorillas: Extraverted, Dominant, Fearful and Understanding (Kuhar, Stoinski, Lukas, & Maple, 2006; Gold & Maple, 1994). The Dominant factor seems to have much less emphasis on unpredictability than in chimpanzees and orangutans, and more emphasis on aggressiveness and irritability. The Fearful factor includes items like *tense*, *eccentric*, and *insecure*. Understanding appears to be a combination of sympathy and nurturing tendencies, and Extraverted reflects social and physical activity.

A recently completed study has used a version of the Great Ape Personality Survey to assess wild Mountain gorillas. At this time analyses are yet unavailable, but preliminary analysis suggests that six Factors, as yet unlabeled, are present (Eckhardt, Steklis, Steklis et al, 2012) in contrast to the previous studies that found four Factors (Kuhar, Stoinski, Lukas, & Maple, 2006; Gold & Maple, 1994). If there are in fact six Personality Factors, it would underscore the value of applying a common or similar measurement of personality in closely related species to detect similarities and differences in their personality structure. Previous studies that had found four factors in gorillas did not use a version of the Great Ape Personality Survey, so comparison between gorillas and chimpanzees and orangutans was complicated by variation introduced by differences in the scales. By using the same or similar scales in assessing personality, we can control for variance arising from differences in the measure being used.

Chimpanzee

Chimpanzees have been the subject of the most extensive research into non-human personality in the great apes (Koski, 2011; Uher, 2011; Dutton, 2008; Schneider & King, 2008; King, Weiss, & Farmer, 2005; Martin, 2005; Penderson, King, & Landau, 2005; Schneider &

King, 2004; King & Landau, 2003; Weiss, King, & Figueiredo, 2000; Gosling, 1999; Lillienfeld, Gershon, Duke, Merino, & de Waal, 1999; King & Figueredo, 1997). As early as the 1920s, Yerkes was writing about differences in the temperament of individual chimpanzees (Yerkes, 1929). In 1949, Hebb proposed that a methodical study of temperament in chimpanzees would be a critical element of understanding human personality (Hebb, 1949). Because chimpanzees and bonobos are our closest extant relatives, sharing a common ancestor with humans roughly 6-7 mya (Varki & Nelson, 2007; Stanford, 1998), comparing personality traits and structure in these two species to human personality traits and structure could reveal traits or elements of personality structure that have been conserved from our last common ancestor.

Studies of chimpanzee personality have included both trait-adjective surveys and behavioral observational ethograms (Koski, 2011; Uher, 2011; Dutton, 2008; Schneider & King, 2008; King, Weiss, & Farmer, 2005; Martin, 2005; Penderson, King, & Landau, 2005; Schneider & King, 2004; King & Landau, 2003; Weiss, King, & Figueiredo, 2000; Gosling, 1999; Lillienfeld, Gershon, Duke, Merino, & de Waal, 1999; King & Figueredo, 1997). In studies employing a version of the Great Ape Personality Survey, six personality Factors were identified in captive common chimpanzees: Openness, Extraversion, Emotional Stability/Neuroticism, Dependability, Agreeableness, and Dominance (King & Figueredo, 1997). Openness consisted of the items *inventive* and *inquisitive*. Extraversion consisted of items including both physical and social activeness like *playful*, *active*, not *solitary*, and not *lazy* (See Appendix A for a list of items in each Factor). Emotionality, or Neuroticism in pessimistic nomenclature, included the items not *unemotional*, not *stable*, and not *excitable*. Dependability is characterized by low impulsivity and low irritability and included items like not *defiant*, not *jealous*, and not *erratic*. Finally, Agreeableness is characterized by thoughtfulness including items like *gentle*, *sensitive*,

and *protective* (King & Figueredo, 1997).

The differences in personality structures among the great apes could reflect adaptations to the different socio-ecological environments and evolutionary pressures of the species.

Orangutans are the most distant of our great ape cousins sharing a common ancestor with the African Great Apes roughly 13 mya (Varki & Nelson, 2007). Gorillas last shared a common ancestor with the *Homo* and *Pan* genera roughly 8 mya (Varki & Nelson, 2007) and the *Pan* and *Homo* lines diverged between roughly 6-7 mya. (Varki & Nelson, 2007; Stanford, 1998).

Similarities in personality structure across species would likely reflect a trait conserved from the last common ancestor, while differences would likely reflect a derived trait, acquired after the speciation event.

In the great ape personality research, chimpanzees and orangutans have personality structures more similar to one another and to humans than the personality structure of gorillas. The differences in personality structure could be an artifact of different measurements used: the studies of chimpanzees and orangutans used versions of the Great Ape Personality Survey while the available gorilla data used a different impressionistic survey. However, the difference in personality structure could reflect the socio-ecological environment of gorillas compared to other great apes. Compared to *Homo* and *Pan*, they do not live in groups with many different males. They generally live in groups with a small number of males. Compared to chimpanzees, there is only rare need to engage in conflicts over dominance rank, and many of those conflicts are resolved by factors like size (Weber & Vedder, 2001; Fossey, 1983). Because there is relatively less competition between males within family groups (Weber & Vedder, 2001; Fossey, 1983), there may be less advantage in being unpredictable than there is for chimpanzees or even orangutans. Also, the emphasis on nurturing is unsurprising for the same reason: most the young

in the group would likely belong to the resident male that increases paternal behaviors.

Chapter 4. Subjective Well-Being (SWB)

SWB in Humans

Subjective Well-Being (SWB) is an operationalization of happiness or contentment and has been studied in psychology, medicine, and sociology (DeNeve, 1999; Diener, Suh, & Oishi, 1997; Huebner, 1991; Lucas, , Diener, & Suh, 1996). SWB is a fundamental interest of human research (Helliwell & Putnam, 2004; Steel, Schmidt, & Schultz, 2008). If one views the goal of the scientific endeavor as the betterment of humanity, then it is arguably the ultimate focus of all research on humans (Steel, Schmidt, & Schultz, 2008). Certainly, understanding what makes people content and happy would make more informed and more efficient public policies and economic and health-care related policies on an institutional level.

In humans, there are at least two major components to SWB in theory: a cognitive component and an emotional component (Huebner, 1991; Lucas, Diener, & Suh, 1996). One of the most commonly used measures of SWB is the Satisfaction With Life Scale developed by Diener and others (see Diener, Suh, & Oishi, 1997 for overview). The Satisfaction with Life Scale measures three domains: satisfaction with life (a cognitive element), positive affect, and negative affect (Deiner, Suh, & Oishi, 1997; Lucas, Diener, & Suh, 1996).

There are many variables that correlate with SWB in humans. Many studies have shown that SWB correlates with personality, health, social relationships and one's genetic predisposition to happiness far more than it does to one's income, social position, or other environmental factors (Camfield, Choudhury, & Devine, 2009; Helliwell & Putnam, 2004).

SWB and personality

An individual's SWB has consistently been found to correlate with elements of their personality (Deiner, Suh, & Oishi, 1997; DeNeve, 1999; Steel, Schmidt, & Shultz, 2008; Weiss,

Bates, Luciano, 2008). In many studies, SWB is positively correlated to Extraversion and negatively correlated with Neuroticism (Deiner, Suh, & Oishi, 1997; DeNeve, 1999; DeNeve & Cooper, 1998; Steel, Schmidt, & Shultz, 2008; Weiss, Bates, Luciano, 2008). SWB is also positively correlated with Agreeableness, Conscientiousness and Openness, though perhaps more modestly so (Deiner, Suh, & Oishi, 1997; DeNeve, 1999; DeNeve & Cooper, 1998; Steel, Schmidt, & Shultz, 2008; Weiss, Bates, Luciano, 2008).

In a meta-analysis of the SWB literature, DeNeve (1999) identified 137 personality traits that had been studied in relation to SWB. DeNeve found that Extraversion and low Neuroticism did correlate with SWB, but not as highly as expected, though a later study by Steel, Schmidt, & Shultz (2008) found the relationships between both Extraversion and SWB, and low Neuroticism and SWB to be even stronger than previous studies. While the magnitude of the relationship between personality and SWB is still being studied, that there are significant relationships is well established.

SWB is correlated with other characteristics as well. SWB is strongly associated with self-reported positive health (DeNeve, 1999; Diener, Suh, Lucas, & Smith, 1999, Helliwell & Putnam, 2004; Weiss, Bates, & Luciano, 2008). In ill health, lower SWB is reported, although the direction of causality, if there is one, is certainly unclear (Diener, Suh, Lucas, & Smith, 1999, Helliwell & Putnam, 2004; Weiss, Bates, & Luciano, 2008). Another trait strongly correlated with SWB is the maintenance of strong, healthy social bonds, and specifically strong social networks and positive social relationships (Caunt, Franklin, Broadatay, & Broadatay, 2012; DeNeve, 1999). Across cultures, the importance of the strength and nature of one's social ties to one's happiness remains strong (Camfield, Choudray, & Devine, 2009).

Research in non-human primate SWB has been driven largely by the desire to improve

living conditions and quality of life for captive non-human primates (King & Landau, 2003), but this research will also deepen our understanding of SWB in humans through a comparative approach. This area of research is still growing, but there have already been some intriguing parallels between human and non-human SWB. For example, in some non-human Great Apes as in humans, there are relationships between SWB and both personality and genetic disposition (Helliwell & Putnam, 2004; Weiss, Bates, & Luciano, 2008). State what this means. Tell us about the relationships you're listing.

SWB in Chimpanzees and Orangutans

In non-humans, the relationship between sociality and SWB (also referred to as psychological well-being) is most salient when individually housed primates display abnormal, sometimes self-abusive behavior (Morton, Kyes, Kyes, & Swindler, 2005). For example, it has been shown that primates housed socially and/or with enrichment toys display fewer abnormal behaviors and more appropriate species-specific behaviors (Morton, Kyes, Swindler, & Swindler, 2005). However, concluding that individuals are happy or contented simply because they are not acting abnormally seems insufficient (King & Landau, 2003; Weiss, King, & Enns, 2002). The Chimpanzee SWB Scale was developed by King & Landau (2003) to assess the presence of SWB, not merely the absence of negative behaviors.

The Chimpanzee SWB Scale was developed from human scales of SWB. This scale has been used, with some small modifications from the earliest forms, in several previous studies of Great Ape personality in chimpanzees and orangutans (King & Landau, 2003; Pederson, King, & Landau, 2005; Schneider & King, 2008; Weiss, Adams, & King, 2011; Weiss & King, 2006; Weiss, King, & Enns, 2002; Weiss et al, 2009). Since researchers cannot ask chimpanzees about the cognitive element of well-being, the scale focuses on raters' assessments of the chimpanzees'

affect. The scale consists of four items modified from the human scale specifically for use with Great Apes (King & Landau, 2003). The four items are rated on a seven-point Likert scale (1: displays either total absence or negligible amounts of the trait or state to 7: displays extremely large amounts of the trait). The first three items measure domains of positive mood or affect, satisfying social interactions, and overall effectiveness in attaining goals. The fourth item is targeted at eliciting a broader assessment. It asks raters how much they would want to be this chimpanzee for a week. This is perhaps as close as researchers can come to a proxy for asking the chimpanzee how satisfied they are with their life.

In chimpanzees, SWB is positively correlated with the Dominance, Extraversion, and Dependability Factors, similar to patterns found throughout the human literature (King & Landau, 2003; Weiss, King, & Enns, 2002). This is similar to the finding that SWB correlates with Extraversion and Conscientiousness in humans (Deiner, Suh, & Oishi, 1997; DeNeve, 1999; DeNeve & Cooper, 1998; Steel, Schmidt, & Shultz, 2008; Weiss, Bates, Luciano, 2008). SWB was also found to be heritable in captive chimpanzees, with an additive genetic heritable estimate of 0.40 (Weiss, King, & Enns, 2002). This estimate is similar to heritability estimates of SWB found in humans (Weiss, King, & Enns, 2002).

SWB has also been found to be correlated to personality Factors in orangutans. In a study conducted on orangutan personality structure, Weiss & King (2006) also administered the four-item Subjective Well-Being Survey. Similar to the findings in humans and chimpanzees, orangutan SWB correlated positively with Extraversion, Agreeableness and negatively with Neuroticism (Weiss, King, & Perkins, 2006). Further, similar to the connection between health and SWB in humans, SWB in orangutans has been shown to predict a longer lifespan (Weiss, Adams, & King, 2011). The similarity across species suggests that the basis of the correlation of

SWB to personality is a trait conserved from at least our last shared ancestor with orangutans. The similarity across species in the correlation of SWB to lifespan not only allows us to infer that it is a conserved trait, but could also aid in directing future human health research and policy.

In previous studies by this author using a version of the four-item Chimpanzee SWB scale, SWB did not correlate with dominance rank (Schneider & King, 2004). However, SWB did positively correlate with the modified Dominance Factor, which excluded the items *dominant* and *submissive* (Schneider & King, 2004). In the same study SWB also significantly positively correlated with Extraversion, Emotionality, Agreeableness, and Openness. Further, SWB was negatively correlated with a bad relationship style (cold, tense, hostile) though it was not correlated significantly with a good relationship style (affable or friendly, calm, and supportive) (Schneider & King, 2004). These findings could either be interpreted as similar to the human findings in that bad relationships go hand in hand with unhappiness, or it could be interpreted as distinct from the human findings in that good relationships are not a correlate of happiness.

Although the relationship between relationship quality and SWB has been studied in humans, in non-humans it has not yet been an area of much research (Caunt, Franklin, Broadaty, & Broadaty, 2012; Proctor, Linley, & Maltby, 2009; DeNeve, 1999). In humans, positive, quality relationships predict higher overall psychological well-being (Cooper, Okamura, & McNeil, 1995). Understanding the potential impact of social experiences of captive animals could have implications for management procedures and tools, as well as animal welfare. As well as aid in animal welfare and a novel tool for theories of the evolution of human sociality by informing the continuing development of the research in human relationships.

Chapter 5. Relationship research

It is hardly exaggeration to say that a chimpanzee kept in solitude is not a real chimpanzee at all. That certain special characteristic qualities of this species of animal only appear when they are in a group, is simply because the behavior of his comrades constitutes for each individual the only adequate incentive for bringing about a great variety of essential forms of behavior. Furthermore, the observation of many peculiarities of the chimpanzee will only be clearly *intelligible* when the behavior and counter-behavior of the individuals in the group are considered as a whole.

Wolfgang Kohler, 1927

The relationships among personality, happiness, and the strength and nature of one's social interactions have proven a fruitful area of investigation in humans. Positive, supportive social relationships are an important predictor of self-reported happiness and SWB (Camfield, Choudray, & Devine, 2009; Caunt, Franklin, Broadatay, & Broadatay, 2012). As mentioned earlier, the connection between SWB and social network support is evident even across cultures (Camfield, Choudray, & Devine, 2009).

For all primates, humans included, affiliative social bonds, especially at the dyad level, are the basis for group cohesion and social structure (Jones, 1984). Positive, supportive, affable relationships between non-kin, or 'friendships', are a universal trait in humans (Blieszner & Adams, 1992; Hruschka, 2010). Friendship and partner preferences begin to emerge in children around the age of three or four years old (Hartrup & Stevens, 1999). Children invoke the word *friendship* to elicit favors and establish bonds quickly (Hruschka, 2010). For example, a child may go up to another and immediately ask to be friends or barter the promise of friendship for some desired resource, say cookies. Spending a short amount of time with children, one becomes familiar with the concept of I'll-be-your-friend-forever-if, if I can have a cookie, play with the toy, etc.

Friendship is also a cross-cultural phenomenon (Blieszner & Adams, 1992; Hruschka, 2010). In ethnographic research friendship has traditionally been ignored in favor of focusing on kin relationships, though it is interesting to note that in the Human Relations Area Files (HRAF) database of ethnographic research there are mentions of five cultures that explicitly and actively discourage friendship as being counter to the good of the community (Hruschka, 2010). In these cultures however, friendships still form in the face of prohibition, taboo, and even penalties (Hruschka, 2010). The importance of social bonds for group cohesion, and the universal nature of friendship in humans make this a critical area of research for understanding social behavior in humans and other social species.

Relationship research identifies two basic units of study simultaneously: the relationship and the individual in the relationship. Researchers can approach the relationship itself as the most basic unit of study, or can focus on characteristics of individuals in the relationship.

The relationship.

Relationships can be characterized in several ways. There is a temporal element: the frequency of proximity, exchange, and interaction, as well as the duration of the relationship. There is the affective element of a relationship: feelings of closeness, affection and trust (Blieszner & Adams, 1992). There is also a cognitive aspect to friendship: thoughts about the other, judgments, perceptions, and interpretations of their behavior (Blieszner & Adams, 1992). There is also a behavioral element: what friends do together, how they communicate, cooperation, reciprocation, and displays of affection (Blieszner & Adams, 1992).

Cross-culturally friendships are marked with certain affective and cognitive traits (Blieszner & Adams, 1992; Hruschka, 2010). Friendships inspire positive affect and demonstrate a lack of jealousy. Further, in friendships, aid and sharing of resources is elicited by

the other's need, not by strict reciprocity (Hruschka, 2010). Friendship also has some common behavioral characteristics across cultures including self-disclosure, informality, frequent socializing, sharing in common activities, emotional support, and the giving and receiving of aid (Hartnup & Stevens, 1999; Hruschka, 2010).

The individual.

One of the central themes in understanding relationships on the level of the individual is variation in individual relationship styles and attachment style (Hruschka, 2010; Nofle & Shaver, 2006). Arising out of Bowlby's early work with infants attachment to their mothers, attachment theory in adults refers to the nature of an individual's close relationships including cognitions, emotions, attitudes and behaviors (Hruschka, 2010; Nofle & Shaver, 2006). Three categories of attachment style have emerged: secure, anxious, and avoidant. Measures of attachment style in adults are used to predict both subjective outcomes in relationships (for example, satisfaction and intimacy) and objective outcomes (for example, divorce) (Hruschka, 2010; Nofle & Shaver, 2006).

Little research has been done in humans comparing attachment style and personality (Nofle & Shaver, 2006; Gleason, Gower, Hohmann & Gleason, 2005). In 1992, a longitudinal study by Shaver & Brennan used both the three categories of attachment style and the Big Five personality factors to predict relationship outcomes and found that attachment style was a better predictor of relationship outcomes than personality (Hruschka, 2010). Since that study in 1992, there has still been a lack of interest in comparing personality and attachment style (Nofle & Shaver, 2006).

Chapter 6. Relationship research in non-human primates

Friendship is the F-word; a word that many primatologists have been reluctant to use in print though we may use it freely when we chat with our colleagues about the animals that we study. When we do use the term in academic venues, we feel compelled to cloak it in italics, as if this gives us some indemnity against charges of anthropomorphism or lack of rigor.

Joan B. Silk, 2002, 421

While in the last few years there have been a growing number of studies into personality and psychological or Subjective Well-Being (SWB) in nonhuman primates (Brune, Brune-Cohrs, McGrew, & Preuschoft, 2007; King & Landau, 2003; Gosling, 2001; Gosling & John, 1999), there have been fewer studies of relationship quality in non-humans (Blieszner & Adams, 1992). Only in the last two decades has the word friendship entered into the primatological discourse (Massen, Sterck, de Vos, 2010; Silk, 2002). And it is only since the early 1990s that the quality of friendships has been recognized as an important area of focus, in addition to the frequency of interactions (Blieszner & Adams, 1992; Cheney, 2010; Massen, Sterck, de Vos, 2010; Silk, 2002). The interest in friendship over the last decade has not only been growing, but also changing focus to include more elements of the emotional aspect of friendship that are such central components of friendship in human research (Cheney, 2010; Massen, Sterck, de Vos, 2010; Seyfarth & Cheney, 2012; Silk, 2002).

It is not that the field was unaware of the importance of friendship in non-human primates. As early as 1986, Goodall provided extensive anecdotal evidence of the strength, stability, and affect of friendships in wild chimpanzees (Goodall, 1986). Even after the publication of Barbara Smuts' classic book *Sex and Friendship in Baboons* (Smuts, 1985) which details the complex and resilient friendships between unrelated adult males and females not engaged in a sexual relationship, any studies using a comparative approach to positive, long-term social bonds between non-kin seem to focus on the material outcomes of that bond (i.e. alloparenting,

coalitions against other group members, food sharing).

Indeed, research in non-human primate relationships often still seems focused on functionally defined relationships (*e.g.* coalitions or associations) and superficially defined measures (*e.g.* proximity as a analogue of friendship in humans) (Massen & Koski, 2014; Silk 2002). A study by Koski and de Vries (2012) assessed relationship quality and stability of social relationships in captive chimpanzees. The authors defined relationships between dyads using a behavioral ethogram approach, scoring behaviors like grooming, approaches, and conflicts (Koski and de Vries. 2012). A more recent study by Massen & Koski (2014) measured social relationships in chimpanzees using both behavioral ethograms and behavioral test/experiments. However, Massen & Koski (2014) still defined friends by physical proximity, specifically contact sitting.

The characterization of friendship in non-human primate research without addressing an emotional component is insufficient, especially in those who focus on comparisons to humans where the emotional component is a critical defining characteristic of friendship. While behavioral ethogram studies are an important aspect of a foundation for non-human research into friendship, for studies of non-human friendship to be analogous to studies of friendship in humans, these studies must include both functional *and* affective elements. Impressionistic trait-adjective surveys may be the best way to capture the affective element of non-human friendship, since these surveys rely on general impressions of the rater across time and many contexts and are not limited to specific behaviors. For the purposes of this paper, the term *friendship* will refer to those relationships with acknowledged affective elements. Adapting and extending human relationship research could be useful to assess the pathology or health of interactions among particular sets of individuals, or possibly to classify individuals in a way that might

predict future behavior.

Studying non-humans in the subtle nuances and variations of their social interactions and relationships will inform our understanding of our own social behaviors and their evolutionary histories. These subtle nuances cannot be fully understood without incorporating that emotional component, and can be of only limited use in comparison to human friendship.

Relationship Style

While characterizing primate groupings by dyads is a common and long-held convention, little has been done to advance our understanding of the affective nature of these relationships, or how variation of an individual's traits might influence the nature and number of their relationships. Relationship style has shown that it may well play a central role in mediating the expression of personality in complex social interactions (Anestis, 2005, 2006; Schneider & King, 2004, 2008). Relationship style may be analogous to attachment style in the human relationship research since attachment style would be the basis for how an individual interacts socially, an individual's attachment style would be related to their relationship style. In the human research there are three theoretically derived styles: anxious, avoidant, and secure. In the studies of chimpanzee relationship style, two common styles have emerged: affiliative and agonistic (Anestis, 2005, 2006; Schneider & King, 2004, 2008). The affiliative relationship style refers to positive social interactions, and agonistic relationship style generally refers to stressful or possibly aggressive social interactions.

A first step in investigating these topics is to understand an individual's relationship style, and what characteristics of an individual influence their social behavior in relationships. A major influence in nearly all aspects of behavior, especially social behaviors, is personality. Anestis (2005, 2006) defined affiliative relationships as hugging, grooming, and proximity, and

agonistic relationships as aggression, displacements, and displays (Anestis, 2005).

Schneider and King (2004, 2008) modified the impressionistic trait-adjective survey method to measure traits of chimpanzee relationships (Schneider & King, 2004, 2008). In that study, affiliative relationship style included the items: *supportive* and *affable or friendly*. Agonistic relationship style included the items: *hostile*, *tense*, and *cold*. Affiliative relationship style was predicted by the personality Factor, Emotional Stability, defined as being stable and not excitable (see Table 1)., Agonistic relationship style was negatively correlated with two personality Factors, Extraversion and Agreeableness (Schneider & King, 2004, 2008). So individual who are had an agonistic relationship style were more socially and physically active and socially sensitive (See Table 1). The current study focuses on the affiliative or agonistic nature of chimpanzee relationships and their relationship to personality, SWB, and demographic variables (age, sex, and dominance rank).

Dyad-level behavior

Dyad-level behaviors are another means of measuring the role of personality in social behaviors. As such, dyadic-level behaviors should be measuring the same latent variable or construct, manifested in a different situation. As with the trait-survey method in personality research, this method is designed to access the cumulative subjective assessments of the raters. They assess each dyad based on their previous experiences across many contexts and over extended time periods. This approach allows for a discrete measure of social behavior arising in part from individual differences, and to use that measure to assess construct validity in the personality and SWB scales.

The current study

The current study focuses on one very general affective characteristic of dyads: whether

the partners like each other (an affiliative relationship) or dislike each other (an agonistic relationship), or if they are essentially indifferent. Most research on primate social relationships has focused on the functional characteristic of the relationships: for example, reciprocity or dominance inequity. It is also common in the primate social relationship research to attempt to explain the formation and nature of primate relationships in terms of individuals' demographic factors: namely, dominance rank, sex, and age. Few studies have investigated the relationship between relationship qualities and individual characteristics like personality (Anestis, 2005).

In this study, relationship quality is measured by a single-score assessment for each dyad. Every dyad an individual is a part of is scored by raters as either liking each other, disliking each other, or indifferent or neutral towards one another. A list of all possible dyad combinations for each zoo can be generated using a nomothetic Social Relations Model (SRM) modified round robin design (Kenny, Kashy, & Cook, 2006). In this design, data are collected on each potential dyad in the population, with each individual being paired with all other individuals (Kenny, Kashy, & Cook, 2006). For example, in a population of four chimpanzees: Bahati, Moshi, Ruby, and Alfie, the dyad list would be: Bahati and Moshi, Bahati and Ruby, Bahati and Alfie, Moshi and Ruby, Moshi and Alfie, Ruby and Alfie.

This method is a modified round robin because data are being collected on the chimpanzee dyads through human raters. This method produces a matrix with data for all *possible* dyadic relationships and forces the raters to think about and assess all possible dyad combinations. The SRM modified round robin approach was chosen for this study because by forcing raters to assess all potential dyads, those dyad combinations that are less salient in the raters' minds will be given the same consideration as those dyads that might 'pop out' or be highly salient to the human observers.

Chapter 7. Current research questions and predictions

Study 1: Reliability of personality and SWB measures over time

The first study focused on reliability of impressionistic trait-adjective scores of personality and SWB for captive chimpanzees. It assessed the reliability of personality and SWB scores of 24 chimpanzees across a ten-year span.

The stability of personality scores over time is challenging to measure in both humans and non-humans because personality develops throughout the lifespan (MacDonald, 2005; Wortman, Lucas & Donnellan, 2012). In an intra-individual study, Terracciano, McCrae & Costa (2010) demonstrated that most serious changes in personality occur in childhood and adolescence and personality stabilizes for the most part in early adulthood. There is evidence in both humans (Soto, John, Gosling, Potter, 2011; Terracciano, McCrae, & Costa, 2010; Asendorpf, 2008; Kwan, John, & Jones, 2002) and non-humans (King, Weiss & Sisco, 2008; Manson & Perry, 2013) of a non-linear relationship between age and personality, though it seems unclear at this time what that relationship looks like. In humans, there has been evidence that personality changes plateau in adulthood (Terracciano, McCrae, & Costa, 2010), though other researchers have found changes in personality traits into late life. (Asendorpf, 2008; Helson, Kwan, John, & Jones, 2002).

In the current study, the reliability of individual chimpanzee personality scores over ten years was assessed by comparing the personality and SWB scores collected in 2013 to scores of personality and SWB taken in 2003. Few, if any, studies have been able to assess test-retest reliability of personality scores for the same individual chimpanzees across such a timespan.

There are several factors that I expect will decrease the reliability of these personality scores. In humans (Soto, John, Gosling, & Potter, 2011; Terracciano, McCrae, & Costa, 2010),

chimpanzees (King, Weiss & Sisco, 2008) and even a new world monkey, the white-faced capuchin (Manson & Perry, 2013), personality undergoes predictable changes across an individual's lifespan. Chimpanzees in this study will have aged ten years, so scores at the two time points could differ due to age effects.

There are additional variables that could decrease correlations between the two time points that would lower the estimates of test-retest reliability. No raters from the original study were used in the recent data collection. Also, many of the chimpanzees have changed zoos, or have had changes in their social group during that time. Many chimpanzees may have experienced changes in their dominance rank. Finally, the raters in 2012-2013 were given a modified version of the original personality survey and there will be fewer items representing each item. All these factors make this perhaps one of the most stringent tests of the reliability of personality scores in non-humans. Even so, I predict that personality scores for all five factors will show moderately high reliability.

SWB varies across lifespan as well in orangutans and humans (Weiss, King, Adams, 2011), and the same changes in social context that might impact the scores of personality would also impact SWB. In humans, strong social bonds and health are predictors of SWB (Caunt, Franklin, Broadatay, & Broadatay, 2012; Cooper, Okamura, & McNeil, 1995; DeNeve, 1999). The chimpanzees could have experienced changes in quality of their social relationships as well as changes in their health as they age. As with the scores of personality, these variables will make this a stringent test of stability of SWB scores. In humans, SWB is stable across time, though less so than personality scores (Fujita & Diener, 2005; Kokko, Korkalainen, Lyyra, & Feldt, 2013). Given the inherent, relatively stable aspect of SWB in humans, I predict a

moderate to high correlation within individuals at both time points, even in the face of the potential changes in the chimpanzees' life.

Study 2: Personality, SWB and dyadic-level behaviors.

The second study focused on establishing the relationship among personality, SWB and one aspect of an individual's behavior in a social setting. Personality underlies a wide range of behaviors, and should be predictive of some behaviors, like dyad quality. The current studies focus on one aspect of relationship quality: whether a pair of chimpanzees like, dislike or are indifferent towards each other. This measure of relationship quality may be a result of demographic variables (age, sex, rank), personality, or subjective well-being (SWB). This study investigates three questions:

Question 1: Do demographic variables predict social behaviors in a dyad?

I predict that an individual's behavior in dyads should correlate with socially relevant aspects of that individual's personality (for example, items like *friendly* and *loving* should correlate with affiliative dyad scores). Further, since personality is the basis for behavior, relevant personality scores will account for more variance in dyad quality than demographic variables alone.

Question 2: Does personality predict social behaviors in a dyad?

While there has been surprisingly little research in humans establishing the relationship between personality and relationship qualities, there are some studies that give a sense of which personality traits may predict relationship quality. In children, popular children were impulsive, recovered from distress quickly, and had less negative affect expression (Gleason, Gower, Hohman & Gleason, 2005). A more recent study of college students in the Greek system or dormitories found that being liked correlated with self-reported traits including talkative, joyful,

and active (Wortman & Wood, 2011). Other traits that correlated with being liked were communal traits, or those that could predict being helpful to others: for example, cooperative, thankful, polite, and practical (Wortman & Wood, 2011). Traits related to dominance were negatively correlated with likeability, for example, assertive, forceful and bold (Wortman & Wood, 2011). Likeability also negatively correlated with irritable, moody, complex/deep, devious, and manipulative (Wortman & Wood, 2011). An individual's personality traits, *i.e.* being social, helpful and not manipulative, result in that individual being liked, being successful in navigating social relationships in this aspect.

I predict that likeability will be positively correlated to Extraversion, Agreeableness, Emotional Stability and Dependability. I predict that dislike scores will be positively correlated to Dominance, and negatively correlated to Emotional Stability and Agreeableness.

However, there is an alternative prediction. A study by Gleason, Gower, Hohman & Gleason (2005) also demonstrated that personality factors may not be appropriate measures of social behavior. In their study, the Extraversion factor included traits that positively correlated with likeability (talkative and energetic/active) and others that correlated negatively with likeability (assertive, forceful and bold). In the current study, personality will be assessed using the personality factors, but also by a second set of personality domains, so an individual's personality is represented without relying on the Factors. Items that are determined *a priori* to predict likeability will be grouped in two scales: the Affability domain scale and the Agonistic domain scale. I predict that the Affable domain scale will correlate positively with likeability, and the Agonistic domain scale will correlate positively with dislikeability.

Question 3: Does SWB predict social behaviors in a dyad?

Given the importance of supportive social relationships in humans, and the general importance of social relationships in chimpanzee daily life, I predict that SWB will correlate positively with likeability and negatively with dislikeability. I predict that SWB may be moderately negatively correlated with neutral dyad scores.

Section II: Methods

Methods

Subjects and Participants

Subjects.

Study 1: Reliability of personality and SWB scores over time. Subjects were 24 chimpanzees (males=10, females =14) with data collected in 2002-2003, and again in 2012-2013. Two surveys of personality were administered during the 2002-2003 study: The ChimpanZoo Ape Personality Assessment Form IA (PAFI) and the ChimpanZoo Ape Personality Assessment II: Adjustment and Emotions (AE). All 24 subjects were scored on the PAFI, but only 9 were scored on the second scale (males=4, females=5). There were 27 chimpanzees with SWB surveys completed in 2002-2003 and 2012-2013 (males=17, females=32).

Study 2: Personality, SWB and dyad-level behavior.

The subjects were 84 captive chimpanzees (*Pan troglodytes*) living in nine zoos in the United States (males=30; females=54). The zoos included in the survey were St. Louis Zoo, Rio Grande Zoological Park, Lion Country Safari Park, Lincoln Park Zoo, Sedgwick Zoo, Oakland Zoo, Little Rock Zoo, Sacramento Zoo, and Asheboro Zoo. Chimpanzees younger than five years of age were excluded from the study because many of their personality traits are as yet not fully developed and their social interactions may be influenced by their age (King, Weiss & Sisco, 2008). The mean age of the remaining chimpanzees was 26.02 years (SD=13.60).

Raters were asked to score dyads in their group in the measure of dyad quality. Only dyads scored by two or more raters were used in the agreement analysis. There were 254 dyads.

Populations.

For this study, the chimpanzees in each zoo were described as a 'population'. For zoos

with segregated groups of chimpanzees not housed together, each segregated group is identified as a population and rated separately. For the 2003 sample, Lion Country Safari Park had three separate populations and Asheboro Zoological Park had two separate populations. In the 2013 sample, Lincoln Park Zoo was the only zoo to have 2 completely separately housed populations, though Lion Country Safari Park usually had 3 separated groups with individuals rotating through the groups. Population sizes ranged from 3 to 19 chimpanzees (see Table 3).

Raters.

Data were collected from five zoos in the U.S. Raters were professional zookeepers, caregivers, or researchers who worked with the chimpanzees. Raters who had known a chimpanzee less than 1 year were excluded from the analysis to ensure that the raters had spent sufficient opportunity to observe the chimpanzee and to have formed an impression of their personalities across time and situations (Phillips & Peck, 2007).

Study 1 The 2002-2003 data had 17 raters. Data were not collected on the amount of time raters had known the chimpanzees, but in informal interviews and verbal instruction zoos were asked only to include raters who were familiar with the chimpanzees being rated.

Study 2 The 2012-2013 data used 35 raters. The average amount of time raters had known the chimpanzees was 7.163 years (median=5 years, SD= 7.2293), with a minimum of 1 year and a maximum of 41 years.

Measures

Data were collected in 3 domains: 1) demographic variables, 2) personality and 3) Subjective Well-Being (SWB).

1. Demographic variables

Age

Study 1. In study 1 age was treated as a continuous variable.

Study 2. Since age has a non-linear relationship with aspects of personality as well as SWB, age was treated as a categorical variable. To preserve sensitivity to the highly relevant effects of age over the lifespan with regard to personality, SWB, and potentially the effect of relationship quality, chimpanzees were grouped into age groups at five-year intervals. There were 9 age groups: five to 10 years old (N=2, male=0, female=2), 10.01 to 15 years old (N=19, male=9, female=10), 15.01 to 20 years old (N=10, male=3, female=7), ages 20.01 to 25 (N=9, male=5, female=4), ages 25.01 to 30 (N=6, male=2, female=4), ages 30.01 to 35 (N=5, male=1, female=4), ages 35.01 to 40 (N=6, male=3, female=3), ages 40.01 to 45 (N=11, male=2, female=9), and those chimpanzees older than 45.01 years (N=6, male=2, female=4).

Dominance rank Raters were asked to provide single vertical hierarchical dominance ranking of all individuals in their zoo's population/s. Raters were asked to rank each chimpanzee in their zoo in order of dominance from 1 (most dominant) to n (least dominant). Scores were then standardized within populations to control for differences in population sizes. For zoos with two or more segregated, independently housed populations, raters were asked to produce separate dominance rankings for each segregated population. Dominance rank was standardized within populations to control for differences in population sizes.

Study 1 Dominance rank data were gathered for all 27 chimpanzees at both time points. In the 2002-2003 data, Asheboro zoo reported two separate groups, and Lion Country Safari Park reported three groups. These were segregated populations with no crossover.

Study 2 In the 2012-2013 data, Lincoln Park Zoo was the only zoo with completely segregated populations and they provided two separate dominance hierarchies. Lion Country Safari Park had a system in place where they usually have two or three groups occupying separate

islands in their exhibit. The individuals in each group are routinely shifted, so most of the chimpanzees have interacted with one another at some point. Two of the four raters for Lion Country Safari Park reported as if there were two separate populations and produced two dominance hierarchies. The remaining two raters used a single dominance hierarchy for all the chimpanzees at the zoo. To maintain the integrity of the raters' observations, I used the 2 groups that had been reported by the first raters to create 2 populations. The rank of individuals relative to one another was maintained by recoding the reported rank to fit into 2 populations. For example, if Hank had been ranked 1 and Juniper had been ranked 2 in the single dominance hierarchy, but were assigned to separate populations, Hank would be ranked 1 in the first population, and Juniper would be ranked 1 in second population.

2. Personality. The current personality survey (Chimponality Assessment 2012) and SWB survey were both developed from earlier versions used in studies of chimpanzees and orangutans (King & Figueredo, 1997; King & Landau, 2003; King, Weiss & Sisco, 2008; Schneider & King, 2004; Weiss & King, 2006; Weiss, King, & Enns, 2002; Weiss, King & Figueredo, 2000).

The Chimponality Assessment 2012 survey consisted of 43 adjectives scored on a seven-point Likert scale. Each item was followed by one or two sentences that defined the adjective. For example, the item *stingy/greedy* was defined with the describing sentences: "*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.*" Raters were asked to refrain from discussing the scale with other raters to allow accurate calculation of inter-rater reliabilities. For each chimpanzee, the mean of each item was taken across raters.

Developing the Chimponality Assessment 2012 survey. The original items used in the 2003 survey were revised to reflect the needs of current study, to continue to develop the surveys, and to remain rater-friendly. Personality surveys and surveys of social behavior for both non-humans and humans were reviewed in the process of revising the survey. Thirty-one of the current items were used in the 2003 study: 25 from the ChimpanZoo Ape Personality Assessment Form IA (PAFI) and 7 from the ChimpanZoo Ape Personality Assessment II: Adjustment and Emotions (AE) (Schneider & King, 2008). Fourteen items were excluded from the ChimpanZoo Ape Personality Assessment Form IA and 14 items were excluded from the ChimpanZoo Ape Personality Assessment II: Adjustment and Emotions, primarily to shorten the measure. Some items were excluded because they were very similar to other items on the survey (e.g. *aggressive* was excluded because it was similar to *hostile*), and some were excluded because they were meant to be measures of psychopathology (e.g. *clumsy*, *depressed*, and *autistic*) that was not investigated in this study.

Modified items. Five items were modified from the original survey. The term *distractible* was changed to *fickle* to refocus the term onto socially significant behaviors. The description remained largely the same, with the terms ‘individuals’ and ‘chimpanzees’ replacing the term ‘tasks’: “*Subject’s focus of attention or concern frequently changes from one individual or group to another as the subject’s attention is divided between different chimpanzees.*”

The item *playful* has been broken down into *playful: other-focused*, referring to playing with conspecifics, and *playful: object-focused*, referring to playing with objects or aspects of the environment like enrichments. Since the focus of this study was on social behavior, it was important to separate the social and physically active aspects of chimpanzee play into separate categories. The descriptive sentence remained essentially the same for both items. *Playful:*

other-focused eliminated the references to play that relied on objects or enclosure features, and *playful: object-focused*, eliminated references to play with other chimpanzees. (*Playful: other-focused: Subject is eager to engage in lively, vigorous, sportive, or acrobatic behaviors with other chimpanzees; Playful: object-focused: Subject is eager to engage in lively, vigorous, sportive, or acrobatic behaviors without other chimpanzees, using objects or surfaces/structures in their environment.*)

The item *manipulative* has been renamed *devious or calculating*. Previously, the item showed low reliability. The term *manipulative* itself may have been too open to judgmental an interpretation to be reliable. A socially strategic behavior may look manipulative to an observer with little affection for an animal, while another observer with a warmer place in their heart for that individual may see the same behavior as savvy or calculated. For a similar reason the item *dependent* was modified to the item *dependent/follower*. The descriptive sentences for both of these items remained the same as in the previous study; only the trait adjective itself was altered. Since both these items are both so socially significant retaining them in an altered form was preferable to excluding them altogether.

Finally, the item *defiant* was changed to *defiant towards humans*. As well as being potentially socially significant, this behavior could have direct implications to the housing and care of chimpanzees. Again, including a modified form of the item was preferable to its exclusion from the survey.

Novel items. There were six items that were not used in the 2003 study. Most of these items were taken from other personality scales in both human and non-human research. They were chosen because of their potential relevance to social behaviors. The items are: *innovative* (King, Weiss, & Farmer, 2005), *popular* (Kuhar, Stoinski, Lukas & Maple, 2006; Gold & Maple,

1994), *nurturing/maternal/paternal* (Kuhar, Stoinski, Lukas & Maple, 2006; Martin, 2005; Gold & Maple, 1994; see Hong & Paunonen, 2008 for summary of Non-Verbal Personality Questionnaire), *insecure* (Kuhar, Stoinski, Lukas & Maple, 2006; Gold & Maple, 1994), *loyal* (Lillienfield, Gershon, Duke, Marino, & de Waal, 1999), *exhibition towards humans* (Lillienfield, Gershon, Duke, Marino, & de Waal, 1999), and *difficulty forming lasting relationships* (Dutton, 2008).

2.1 Personality Factors. In previous studies using Principle Components analysis, six personality factors were identified in chimpanzees: Dominance, Extraversion, Emotional Stability, Conscientiousness, Agreeableness, and Openness (King, Weiss, & Farmer, 2005, Pederson, King, & Landau, 2005, King & Figueredo, 1997). Twenty-six of the 43 adjectives used in the Chimponality 2013 scale were previously part of the ChimpanZoo Ape Personality Assessment Form IA, have already been Factor Analyzed, and it is known which Factor on which they have a salient loading (see Table 1). In this study, only one item had loaded previously on the Openness Factor, so Openness was excluded from the analyses. The novel and modified items were not included in the analyses of the personality factors.

Since the personality scales were shortened from the original forms, the resulting factors contain fewer items than in the previous studies. The Dominance Factor consisted of 9 items: *dominant, submissive, independent, intelligent, bullying, stingy/greedy, fearful, timid, and dependent/follower*. The Extraversion factor consisted of 5 items: *active, social, friendly, affectionate, and solitary*. The Conscientiousness factor consisted of 4 items: *predictable, reckless, aggressive, and jealous*. The Agreeableness factor consisted of 5 items: *sympathetic, helpful, protective, and gentle*. The Emotional Stability factor consisted of 2 items: *stable and excitable*.

2.2 Sociality domains. While the personality Factors are one way to organize the items in the personality scale, this study was specifically focused on predicting an individual's affiliative or agonistic behavior in social interactions in dyads. Findings from the previous study by this author (Schneider & King, 2008, 2004) and research by Anestis (2006) supported developing two distinct dimensions of dyadic social behavior: positive/affable and negative/agonistic. In a separate analysis, certain socially relevant items from the entire Chimponality 2012 survey were selected *a priori* and grouped into two domains reflecting dimensions of social behavior.

Affability domain scale. The Affability subscale was constructed *a priori* from items on the Chimponality 2012 scale that would reflect positive social interactions, including 11 items: *friendly, affectionate, sympathetic, helpful, protective, gentle, loyal, popular, loving/caring, cooperative, playful: other-focused* (See Table 2). For each chimpanzee, the mean of these items was taken across raters.

Agonistic domain scale. The Agonistic subscale was also constructed *a priori* from items on the scale that would reflect negative social interactions, including 6 items: *bullying, stingy/greedy, jealous, fickle, hostile, devious/calculating* (See Table 2). For each chimpanzee, the mean of these items was taken across raters.

3. Subjective Well-Being (SWB). The subjective well-being scale was developed specifically for use with great apes and has been used in several previous studies of great ape personality (Weiss, King, & Adams, 2011; King & Landau, 2003; Weiss, King, & Enns, 2002). The SWB scale consists of 4 items, rated on a seven-point Likert scale (1=Displays either total absence or negligible amounts of the trait or state; 7= Displays an extremely large amount of the trait). Each item consists of one or two sentences describing an aspect of SWB.

The first item assesses overall time the chimpanzee is in a good mood: *Estimate the amount of time this chimpanzee is happy, contented, enjoying itself or otherwise in a positive mood. Assume that at other times the chimpanzee is unhappy, bored, frightened, or otherwise in a negative mood.*

The second item scores how satisfying and enjoyable social interactions are for the chimpanzee: *Estimate the extent to which social interactions with other chimpanzees are satisfying, enjoyable experiences, as opposed to being a source of fright, distress, frustration, or some other negative experience. It is not the number of social interactions that should be estimated, but the extent to which social interactions that do occur are a positive experience. Use all social interactions of the chimpanzee as a basis for your judgment.*

The third item measures how effective the chimpanzee is in achieving its goals: *Estimate the extent to which this chimpanzee is effective or successful in achieving desired social interactions, achieving a desired dominance status, and having access to desirable locations, devices, or materials in the enclosure. Each chimpanzee will presumably have its own set of goals different from those of other chimpanzees.*

The fourth item is the most distinct from human measures of SWB. It asks the rater to imagine that they could choose to be one of their chimpanzees for a week. They are asked to score, if that were possible, how much they would want to be this chimpanzee: *Imagine that you could be one of the chimpanzees in your zoo for a week. You would be exactly like that chimpanzee. You would behave the same way as that chimpanzee, would perceive the world the same way as that chimpanzee, and would feel things the same way as that chimpanzee. How much would you want to be this particular chimpanzee?*

In the 2002-2003 survey, raters were asked to rank the chimpanzee that most fit that item's description at 1 and the chimpanzee that least fit the item at 7, and rank the others in the group between the two. In later versions of the SWB scale, this ranking system was changed to a 7 point Likert scale where the rater was asked to assess how well each statement described a given chimpanzee.

A single SWB score for each chimpanzee was defined as the mean of the four items across raters. Each chimpanzee's score was defined as the mean across raters.

4. Dyad Attributes. By using a modified Round Robin design, I generated a list of each possible dyad combination for each zoo population (Kenny, Kashy, & Cook, 2006). Raters were asked the following question: "For each dyad combination below, please indicate whether the chimpanzees in the dyad overall: like each other, seem neutral, or dislike each other. If you do not know, you may check the box next to 'I don't know'".

Three dyad attribute scores were scored for each chimpanzee: *liking each other*, *neutral towards each other*, or *disliking each other*. For each chimpanzee-rater combination, I calculated the number dyads that were scored as *liking each other*, *disliking each other*, and seeming *neutral/indifferent towards one another*. The means were calculated across raters to produce one score for each chimpanzee for liking, disliking, or neutral dyads. Since the number of potential dyads varies as a function of the population size, the average number of like dyads, dislike dyads, and neutral/indifferent dyads for each chimpanzee were then divided by the mean number of relationships reported for that chimpanzee to produce a proportion of dyads that were rated as like (LK), dislike (DK), or neutral/indifferent towards each other (NT). While these three measures are not independent of one another, each was analyzed separately since it is

unknown how the three variables may vary. For example, with an individual's LK score alone, neither their DK nor NT score could be determined.

Statistical Analyses

Statistical analyses were done using PASWStatistics (version 18; SPSS Inc., Chicago, IL).

Study 1 The correlation between variable scores at both time points was defined by Pearson's r correlation coefficient.

Study 2

Inter-rater reliability In studies of non-human personality, Inter-Class Correlations ICC (3,1) and ICC (3,k) are commonly used to calculate inter-rater reliability (Tetley & O'Hara, 2012). Shrout & Fleiss (1979) first proposed the inter-class correlation to assess inter-rater reliability in cases where multiple subjects (n) are scored by multiple raters (k). They proposed three cases for this type of study: 1) each target is rated by a unique set of raters, 2) every subject is rated by the same selection of raters, and 3) each subject is rated by the same subset of k raters (Shrout & Fleiss, 1979).

This study falls into the category of the third case: subjects at the same zoo were scored by the same set of raters. There are two inter-class correlations relevant to this study. The first is ICC (3,1):

$$ICC(3,1) = (BMS - EMS) / BMS + (k-1)EMS$$

where:

BMS = mean squares between chimpanzees,

EMS = mean squares for the chimpanzee by rater interaction, and

k = the mean number of raters per chimpanzee.

A General Linear Model (GLM) Type III was used to generate the means squares values for the equation with the target variable as the dependent variable and the chimpanzee and rater terms as the independent variables. For example, the following GLM was used to calculate the mean squares for the Agreeableness Factor:

$$\text{Agreeableness Factor} = \text{chimpanzee} \text{ rater} \text{ chimpanzee} * \text{rater} / \text{ssIII}$$

In ICC (3,1), the reliability estimate is an estimate of rater consistency for individual raters rather than reliability of scores of variables (Shrout & Fleiss, 1979). This estimate is most useful in comparing reliability estimates across studies.

The second reliability estimate takes into account the mean number of raters scoring the variable (Shrout & Fleiss, 1979). ICC (3,k) gives an estimate of the reliability of mean scores across raters. This is the relevant score to assess the reliability of the variables in this study. The equation for this estimate, ICC (3,k), is:

$$\text{ICC (3,k)} = \text{BMS-EMS/BMS}$$

Agreement Scores There were three potential scores for each dyad. For each dyad, I calculated the proportion of raters who agreed on a score, potentially ranging from 0 to 1.00. For example, if the dyad of Maria and Pablo were scored by four raters as: *liking each other*, *liking each other*, and *neutral towards one another*, and *liking each other*, the agreement score for the dyad would be three out of four or 0.75. If the dyad had been rated as: *liking each other*, *liking each other*, *neutral towards one another*, and *neutral towards one another*, the agreement score would have been 0.5. Dyads rated by only one rater were excluded from this analysis. The proportion of agreement was taken from the dyads that had been rated as *liking each other*, *disliking each other*, or *neutral towards each other*. In the larger zoos with semi-segregated populations, not all raters had observed all possible dyad combinations. These raters scored

these dyads *I don't know* or skipped the item. Dyads that had been rated as *I don't know* were treated as missing data. There were 254 dyads used in the agreement score analysis.

General Linear Models

Demographic variables. Dominance rank, age, and sex are potentially relevant variables in social behaviors. Indeed, there may be many primatologists who would assume that most social interactions between individuals could be categorized/understood/explained in terms of these variables alone. Many dyadic interactions may be affected, especially in chimpanzees by the individuals' age, rank, and sex. For each LK, DK, and NT, I ran a GLM with Type III Sums of Squares using age, rank and sex as the predictors and two-way interactions between rank, sex and age. For example:

$$\text{LK} = \text{age sex rank age*sex age*rank sex*rank/ss3}$$

Personality Factors. For each LK, DK, and NT, I ran a GLM with Type III Sums of Squares using age and sex, Dominance Factor, Extraversion Factor, Dependability Factor, Agreeableness Factor, and Emotional Stability Factor as the predictors and two-way interactions between sex and age and the Factors. For example:

$$\begin{aligned} \text{LK} = & \text{age sex age*sex Dominance Extraversion Dependability Agreeableness Emotional} \\ & \text{Stability Dominance*age Dominance*sex Extraversion*age Extraversion*sex} \\ & \text{Dependability*age Dependability*sex Agreeableness*age Agreeableness*sex Emotional} \\ & \text{Stability*age Emotional Stability*sex/ss3} \end{aligned}$$

Sociality domains: Affability and Agonistic. Similar to the equations using the personality factors, I ran GLMs with Type 3 Sums of Squares using age, rank, sex and the Affability or Agonistic domain score, and the 2-way interactions between age, sex, rank, and Affability or Agonistic score. For example:

LK= age sex rank Affability age*sex age*rank sex*rank Affability*age Affability*sex
Affability*sex/ss3

and

LK= age sex rank Agonistic age*sex age*rank sex*rank Agonistic*age Agonistic*sex
Agonistic*sex/ss3

Subjective Well- Being (SWB). For each LK, DK, and NT, I ran a GLM with Type III Sums of Squares using age, rank and sex, and SWB as the predictors and two-way interactions between sex, rank and age and SWB. For example:

LK= age sex rank SWB age*sex age*rank age*SWB sex*SWB sex*rank rank*SWB/ss3
Are personality and SWB stable across time?

Ethical consideration

The research proposal for this study was approved by the Chimpanzee Species Survival Plan research committee. Individual zoos were then contacted and asked to take part in the study. For those zoos that have research committees, the research proposal was then submitted for zoo review and approval.

Section III: Results Study 1 and Study 2

Results

Study 1: Reliability of personality and SWB scores over time. Dominance rank was stable over the ten-year timespan ($r=0.338$, $p=0.023$) (See Table 3). Only two of the Factors were significantly correlated across the ten year interval: Dominance ($r=0.723$, $p<0.001$) and Agreeableness ($r=0.422$, $p=0.040$). SWB was not correlated significantly between the two time points. Individual items were also compared at the two time periods.

Dominance Factor. The Dominance Factor contained eight items, seven of which were statistically significantly positively correlated: *dominant* ($r=0.773$, $p<0.001$), *fearful* ($r=0.682$, $p<0.001$), *timid* ($r=0.592$, $p=0.002$), *independent* ($r=0.557$, $p=0.006$), *submissive* ($r=0.447$, $p=0.029$), *intelligent* ($r=0.440$, $p=0.031$), and *bullying* ($r=0.420$, $p=0.041$). The item *stingy/greedy* was not statistically significantly correlated between time points.

Agreeableness Factor. Agreeableness was correlated between the two time points ($r=0.422$, $p=0.040$). The Agreeableness Factor was comprised of five items: *sympathetic*, *sensitive*, *helpful*, *protective*, and *gentle*. Only the item *gentle* correlated between the two time points significantly ($r=0.566$, $p=0.004$). If the item *gentle* is removed from the Agreeableness Factor, it no longer shows a significant correlation between the two scores ($r=0.294$, $p=0.163$).

Extraversion Factor. The Extraversion Factor was not statistically significant, nor were any of the individual items in the Factor.

Dependability Factor. The Dependability Factor was not significantly correlated between the two time points, and only one of its items showed a significant correlation. The item *reckless* correlated between the two scores ($r=0.493$, $p=0.036$).

Emotional Stability Factor. The Emotional Stability Factor was not correlated between the two periods. This factor only contained two items: *stable* and *excitable*. The item *stable* correlated with itself ($r=0.422$, $p=0.030$), but the item *excitable* did not.

Non-Factor items. There were items included in the study that were not part of the Factors. These items included: *loving/caring*, *hostile*, *cooperative*, *socially perceptive*, *peacemaker*, and *happy*. Of these six items, three showed a statistically significant correlation: *hostile* ($r=0.752$, $p=0.019$), *cooperative* ($r=0.729$, $p=0.026$), and *socially perceptive* ($r=0.716$, $p=0.030$). The items *loving/caring*, *peacemaker* and *happy* did not correlate between time points.

Subjective Well-Being. SWB scores did correlate between time points ($r=0.390$, $p=0.044$). Of the four items in the SWB scale, only one showed a correlation between time points, *effective at achieving their goals* ($r=0.659$, $p<0.001$).

A note on alpha slippage. In executing a long string of correlations, there is an increased likelihood of a Type I error, results indicating a statistically significant result where there is no actual effect. This study is an exploratory study: there are no other studies similar to it to indicate what relationships might be expected. To explore the nature of the data gathered, without a clear indication of direction from previous studies, more analyses are required than would be used in a more targeted study. Further research will demonstrate the reliability of these each of these findings.

Study 2: Personality, SWB and dyad-level behavior.

Inter-rater reliability 2012-2013. Inter-rater reliability scores for each zoo are reported in Tables 4.1-4.6. Overall inter-rater reliability scores are reported in Table 5. The mean inter-rater reliability score, ICC(3, k), for the Dominance factor was 0.6621 (SD=0.8011), Extraversion was 7.5630 (SD=4.6906), Dependability was 0.6548 (SD=0.2926), Agreeableness was 0.5282

(SD=0.3910), and Emotional Stability was 0.5730 (SD=0.4437). The mean ICC(3,*k*) for SWB was 0.4431 (SD=0.9893).

Inter-rater reliabilities were calculated for the LK, DK, and NT variables across zoos (see Table 5). The ICC(3,*k*) for LK was 0.5811, DK was 0.5714, and NT was 0.5902.

These reliability estimates were adequate and similar to those found in other studies. The inter-rater reliability between zoos (see Tables 4.1-4.6) could be attributed to noise due to the relatively small sample sizes.

Agreement Scores There were 254 dyads used in the agreement score analysis. The mean agreement score was 0.80 (SD=0.20), with a minimum of 0.33 and a maximum of 1.00. Out of the 254 dyads, 240 (94.49%) had an agreement score of 0.5 or higher and 194 (76.64%) had an agreement score of 0.67 or higher.

Question 1: Do demographic variables predict social behaviors in a dyad?

Females had both significantly lower LK scores than males [$F(73)=4.173$, $p=0.045$] and lower DK scores than males [$F(73)=17.934$, $p<0.001$]. The LK mean score for females was 67.3580, and the mean LK score for males was 74.7959. The DK mean score for females was 3.6859 and for males was 5.5695.

As age increased, LK decreased [$F(73)=6.348$, $p=0.014$]. There was also an age*sex interaction for both LK and DK [$F(73)=5.331$, $p=0.024$ and $F(73)=13.876$, $p<0.001$ respectively]. As females age, they are less liked and more disliked (see Figure 1 and Figure 2). Males seem to have a developmental peak of dis-likeability between the ages of 8-25, after which their DK scores drop drastically. At the same time, around the age of 20, males' LK scores increase noticeably (see Figure 1 and Figure 2).

The demographic models were run again for LK and DK, analyzing male and female

chimpanzees separately. For females, age alone was significant in the models for LK and DK [$F(46)=4.321$, $p=0.044$], and $F(46)=5.445$, $p=0.024$), respectively]. Rank had no impact on whether females were liked or disliked, but as they age, females' relationships become both less positive (lower LK scores) and more unpleasant (higher DK scores).

Males with high rank were more liked ($F(26)=5.221$, $p=0.032$) and less disliked ($F(26)=4.479$, $p=0.045$). Older males were more liked than younger males ($F(26)=4.479$, $p=0.045$), and were less disliked than younger males ($F(26)=6.478$, $p=0.018$).

None of the variables were significant in the GLM for NT scores.

Question 2: Does personality predict social behaviors in a dyad?

Personality Factors. Personality factors did not predict LK or DK scores. No main effects for personality factors were significant within any of the three models (LK, DK, or NT). There was a significant interaction between age and the Emotional Stability factor for NT [$F(80)=3.996$, $p=0.050$].

Sociality domains. Both the Affability and Agonistic domain scales demonstrated internal consistency. The Affability subscale had a Cronbach's alpha coefficient of 0.875. The Agonistic subscale had a Cronbach's alpha coefficient of 0.848.

Likeability was positively related to affable personality types, but not agonistic personality traits. For LK, the Affability scale was significant [$F(73)=10.187$, $p=0.002$]. The Agonistic scale was not significant.

DK was not predicted by either affable, friendly personality traits or disagreeable personality trait. For DK, neither the Affability scale nor the Agonistic scales were significant.

NT individuals are not affable, friendly or outgoing. Individuals who scored high in NT scored low on the Affability scale [$F(73)=7.173$, $p=0.009$]. The interaction between rank and the

Agonistic scale was significant in the NT GLM [$F(73)=4.736$, $p=0.033$], although there was no main effect for the Agonistic scale. High rank buffers the impact of an agonistic relationship style on social interactions. Individuals who are mean and selfish, but have high rank are still interacting with other individuals. On the other hand, individuals who are agonistic but are not buffered by the enticements that come with high rank are not interacting with other chimpanzees.

Question 3: Does SWB predict social behaviors in a dyad?

There were no main effects for SWB in the analysis for LK. LK was predicted by the sex by SWB interaction as well as the sex*rank interaction [$F(73)=5.354$, $p=0.024$, and $F(73)=7.482$, $p=0.008$ respectively]. The model was run again, separately for males and females, but no variables were significant in the analysis for LK for males or females.

Happy individuals were not less disliked. SWB was significant in neither analyses.

Follow-up question: What is NT?

Raters were given two choices in addition to rating the dyads as liking or disliking one another. They could indicate, "I don't know", thereby choosing not to rate the dyad. The other option was to rate the dyad as neutral towards each other. Unlike LK or DK, NT was not predicted by demographic variables or SWB, but both the Affability subscale and the interaction of the Agonistic subscale with rank were significant in predicting NT (Affability inversely, Agonistic positively). This result suggests that NT scores are describing a trait of individuals, and are measuring some trait distinct from LK and DK. To explore the nature of NT, a correlation matrix was produced using Pearson's r correlation coefficients. All items in the Chimponality 2012 scale were included in the correlation matrix; only those that were significant are described.

Through the correlation matrix, it becomes apparent that high NT individuals are less social overall. NT scores negatively correlated with LK ($r=-0.932$, $p<0.001$) but did not correlate significantly with DK. Also, NT correlated negatively with rank: high rank indicated low NT scores ($r=-0.364$, $p=0.001$). When analyzed separately this remained true for males ($r=-0.599$, $p=0.001$), but not for females. Having a less socially oriented personality does not impact female rank, but males with a less social personality find it more difficult to propel themselves up the hierarchy.

The correlations between high NT and personality items reveal that high NT is an indication of a syndrome of social maladjustment in captive chimpanzees. This syndrome has four aspects: 1) not socially active, 2) insecure and powerless, 3) un-personable and unlikeable, and 4) lacking in social acumen or intelligence.

1) The first cluster of items directly influence how often one interacts with others or has the opportunity to interact with others. The 3 items are: *solitary* ($r=0.439$, $p<0.001$), *sociable* ($r=-0.366$, $p=0.001$) and *active* ($r=-0.356$, $p=0.001$), all items that are part of the Extraversion factor. Scoring high on the items *solitary* and low in the item *sociable* are ostensibly measures of the frequency with which one has interactions with other chimpanzees. Scoring low on the item *active* would indirectly impact the frequency with which one can interact with other chimpanzees by limiting the chances to encounter other chimpanzees.

2) The second group of items indicates insecurity or lack of control over one's social environment. The 4 items are: *dominant* ($r=-0.339$, $p=0.002$), *insecure* ($r=0.335$, $p=0.002$), *fearful* ($r=0.284$, $p=0.010$) and *submissive* ($r=0.261$, $p=0.019$). Clearly, these items relate to one another. If one is high in *dominant* and low in *submissive* one would not act in a fearful or insecure manner.

3) The third set of items reflects an un-personable tenor to one's interactions with others. These 7 items are: not *playful other-focused* ($r=-0.503$, $p<0.001$), not *happy* ($r=-.406$, $p<0.001$), not *playful object-focused* ($r=-0.360$, $p=0.001$), not *friendly* ($r=-0.262$, $p=0.018$), not *loving/caring* ($r=-0.250$, $p=0.025$), not *affectionate* ($r=-0.220$, $p=0.049$), but *predictable* ($r=0.218$, $p=0.050$). Individuals who score high in NT are grumpy, sad, and cold, but they are consistently so.

4) The last group of 11 items indicates a lack of social savvy and social intelligence. These items include: not *popular* ($r=-0.518$, $p<0.001$), not *innovative* ($r=-0.403$, $p<0.001$), *difficulty forming lasting relationships* ($r=0.398$, $p<0.001$), not *intelligent* ($r=-0.395$, $p<0.001$), not *socially perceptive* ($r=-0.378$, $p<0.001$), not *devious/calculating* ($r=-0.340$, $p=0.002$), not *loyal* ($r=-0.321$, $p=0.003$), not *cooperative* ($r=-0.296$, $p=0.007$), not *helpful* ($r=-0.248$, $p=0.026$), not *peacemaker* ($r=-0.235$, $p=0.035$), and *defiant to humans* ($r=0.220$, $p=0.049$). High NT individuals are less smart than others as indicated by the items *intelligent*, *innovative*, and *socially perceptive*. They are also less adept at some basic chimpanzee social skills. These chimpanzees not only lack positive social skills like being loyal, cooperative, helpful, and being a peacemaker; they also lack the Machiavellian, scheming aspect central to chimpanzee social life, measured by the item *devious/calculating*. The social awkwardness of these chimpanzees is reflected in the items *popular* and *difficulty forming lasting relationships*. They cannot properly or successfully interact with other chimpanzees if they do not have the basic tools necessary to forge a place in chimpanzee society.

This paints a portrait of the high NT individual sitting off from the group by themselves rarely moving about or playing, cowering from interactions with others who are inevitably higher

in rank, socially inept or clueless, and reticent on the rare occasions he/she does interact with others to make themselves vulnerable with kindness or overtures of friendship.

Profile of an NT chimpanzee. I used another method of investigating these individuals with relatively high NT scores. The range for NT scores (as a proportion of reported dyads) was 0.00 to 75.00, with a mean of 25.50 and a standard deviation of 18.35. I compared individuals with NT scores one standard deviation above the mean, above 43.85 (N=9), and those subjects with scores one standard deviation below the mean, below 43.85 (N=72), using a one-way ANOVA. Chimpanzees high in NT were statistically significantly lower in rank [$F(72)=8.285$, $p=0.005$], though there was no significant difference in age between the groups. High NT chimpanzees were lower in SWB [$F(79)=10.053$, $p=0.002$]. They scored significantly lower in the Dominance Factor [$F(79)=8.289$, $p=0.005$] and in the Extraversion Factor [$F(79)=19.130$, $p<0.001$]. There was no difference in the other personality factors. High NT chimpanzees were also rated higher on the Affable Domain scale [$F(79)=24.237$, $p<0.001$], but there was no difference on the Agonistic Domain scale. This view also supports the portrait of unsociable, socially unsophisticated, unhappy chimpanzees.

Section IV: Discussion Study 1 and Study 2

Discussion

Study 1: Reliability of personality, SWB and dyad-level behavior over time.

Personality Factors. Only two of the factors (Dominance and Agreeableness) showed a statistically significant correlation between scores in the 2002-2003 data and the 2012-2013 data. The other factors had Pearson's correlation coefficients ranging from 0.261 (Extraversion) to 0.339 (Emotional Stability). While not statistically significant, the correlations coefficients for the other four factors were roughly similar to measures of stability in personality in humans (Gosling, Renfrow, & Swann, 2003). The lack of significance in the correlations between both some personality factors and SWB across time could be a result of a small sample size (min=9, max=27). A larger sample would have been preferable, but death, exclusionary factors, or transfer to a non-participating zoo limited the potential sample size. For this study novel data were collected on 84 chimpanzees, so in the future a larger sample may be possible.

There were, of course, several factors that decrease the likelihood of finding correlations between scores at the two collection points. Before beginning the study, many potential sources that might depress inter-rater reliability were known: use of different raters, changes in social group composition, individuals being moved between zoos, and changes in personality across the lifespan. Also, the sample size was low. Data were gathered on at most 47 chimpanzees (for dominance rank scores), to only 9 chimpanzees (for the items from the ChimpanZoo Ape Personality Assessment II: Adjustment and Emotions survey), with the personality factors being drawn from data gathered on only 24 chimpanzees. The small sample size, in addition to the other variables, may have made the results too unreliable to draw conclusions. From this sample

alone, it would be premature to conclude that the scores themselves are changing significantly over time.

It is worth noting that the two Factors that were significantly were the largest and second largest factors: Dominance, 7 items; Agreeableness, 6 items. These two items were less effected by the small sample size than the other Factors (See Table 2), and therefore they were less susceptible than the smaller Factors to a Type II Error, failing to find a relationship between variables where there is one. This also supports the need for research with a larger sample size before any conclusions are drawn about the temporal reliability of chimpanzee personality scores.

Dominance rank. Dominance rank was remarkably stable for a ten-year timespan. While we might expect a more changeable hierarchy in chimpanzees in the wild, in captivity several factors likely contribute to the static nature of hierarchy (de Waal, 1982). Captive chimpanzees have no alternative to leave the group. This is an obvious point, but the impact of this aspect of captivity is broad. In informal interviews with keepers, several described the stability of dominance hierarchies for long periods of time (personal communication). The introduction of some new element commonly precedes changes in the hierarchy, such as the introduction of new individuals to the group or a juvenile group member maturing to adulthood. These changes are relatively infrequent. These types of changes, and others such as fertility and estrus, are also closely monitored and even controlled by zoo staff, potentially further increasing the stability of the group.

The stability of dominance rank may be contributing to the high correlation between the Dominance factor at both time points, or vice versa. It is not clear from this analysis, however, if one trait is responsible for causing the other or if they are co-occurring as the result of some other, as-yet-unidentified trait. Dominance rank is highly correlated with the Dominance factor

(Schneider & King, 2008), and so stable rank would be expected to correlate with a stable Dominance Factor. Further research is needed to determine if stability in rank is confounded with stability in the Dominance Factor, if they are both part of a general latent variable, or if both variables simply demonstrate high reliability over time. Research into the potential affect of dominance rank's stability on the stability of the Dominance factor over time should likely employ wild populations where social stability of a group is not monitored and controlled by human intervention. There seems to be no other pattern in which items show reliability over time.

Study 2: Personality, SWB and dyad-level behavior.

In interpreting the results of these analyses, one should keep in mind that in captivity, populations are relatively small compared to wild populations and it is too soon to draw conclusions about the generalizability of these findings to wild populations (de Waal, 1986, 1982). The small population size combined with externally imposed group assignment may constrain the amount of change in the group, as well as the amount of aggressive behavior. Zoo populations are also artificially constructed, usually to meet the capacities of zoo facilities and avoid inbreeding with little attention paid to other aspects of chimpanzee life. In many ways, chimpanzees in zoos are much like children in school classes. They have no choice where they are assigned to reside, they do not have an option to leave the group, and there are powerful figures (teachers or keepers) constantly vigilant to intervene in any social interaction that may be too extreme.

Keepers attempt to allow their charges to have the most naturalistic experiences possible, including aggression and social upheaval, but the fact remains that there are boundaries surrounding captive chimpanzees. Their behavioral extremes are suppressed by their

conspecifics by the necessity of getting along with small number of individuals for years on end. At the same time, their behaviors are suppressed by caregivers who cannot allow some of the horrors chimpanzees inflict on one another in the wild. We would expect under these conditions that chimpanzees' social preferences would be greatly constrained; however, even in these unfavorable conditions, individual differences in social behavior were still found.

Question 1: Do demographic variables predict dyadic-level behavior?

The social relationships of female chimpanzees are less affectively extreme than that of male chimpanzees. Female chimpanzees were both less liked and less disliked than their male counterparts (see Figure 1 and Figure 2). The variables influencing the likeability of males and females are different as well. Females' likeability depends on their age: females are less liked and more disliked as they aged. For males, both rank and age are important factors in both likeability and dis-likeability. Low ranking males were less liked and more disliked than high-ranking males. Males were also liked more and less disliked as they aged (See Figures 1 and 2).

The differences between males and females in the demographic variables influencing relationship quality make sense in light of the different lifestyles of male and female chimpanzees. For male chimpanzees, an individual's rank and the rank of his closest associates, is the center of daily life. In the wild, male chimpanzees form a single vertical dominance hierarchy (de Waal, 1982; Goodall, 1986; Parish, 1994). Unlike many other primates, chimpanzees are patrilocal, meaning that the males remain with their natal group while females will leave the group at sexual maturity to join another social group (Goodall, 1986; Wrangham, 1980). Male chimpanzees in the wild live among their male kin, allowing for males to cooperate with kin and increase their inclusive fitness. However, male bonding in chimpanzees goes beyond patriline affiliation. To achieve high rank, males must often form alliances with other

males, spending time together, grooming and helping one another in social conflicts (de Waal, 1982, 1986; Goodall, 1986; Stanford, 1998).

On the other hand, female chimpanzees in the wild form a loose, horizontal dominance hierarchy, meaning pairs of females have a dominance relationship with one another, but there is not a cohesive singular rank. Female chimpanzees in the wild do not spend much time interacting with one another, but rather spend most their time foraging and resting on their own or with their young. In captivity food provisioning relieves females from the twin burdens of foraging stress and resource competition (de Waal, 1986; Parish, 1994). Under these conditions, female chimpanzees spend much more time socializing and in close proximity to one another and to males, and they also form a more recognizably vertical dominance hierarchy (de Waal, 1982). It would seem, however, that the mechanisms or critical factors for females in these close relationships are different than it is in male chimpanzees. While males were valued for dominance, females were valued for youth.

As females get older, they are less liked and more disliked. This seems counterintuitive in many ways. Older female chimpanzees are preferred as mating partners by males (Proctor, Lambeth, Schapiro, & Brosnan, 2011). In captivity, many females are kept on contraceptives to prevent unplanned pregnancy, so with fertility signals suppressed, older females may no longer benefit from enhanced sexiness. Younger females could be more liked and less disliked because they have no adult or juvenile offspring in the group that may require their mother's support. Perhaps mothers' support of their older offspring as they begin establishing themselves causes friction with other members of the group.

For males, both age and rank were important in both like and dislike scores. As males age they are more liked and less disliked. Based on informal interviews and discussions with

keepers, it is common for male chimpanzees that are entering adulthood to become more troublesome and disruptive as they get bigger and to try to make a place for themselves in the group's adult dominance hierarchy. This would explain the pattern we see in Figures 1 and 2: m dis-likeability peaking in early adolescence and young adulthood, and likeability increasing in mid-adulthood and then remaining stable. As males become older, they are no longer seeking out or involved in frequent skirmishes over rank, therefore, they would have fewer agonistic relationships and be involved in fewer DK relationships. This scenario would also include a tendency for male rank to increase with age (Schneider & King, 2004). Fully adult males would have an established rank, would need to prove themselves less, and would have the opportunity to be more congenial in general. This could be tested by comparing males with relatively more established rank to males of the same age whose rank is not yet established.

Once males get over getting their dander up at every imagined slight, their social life becomes more relaxed. Females, however, have only the long, slow, inevitable slide into ignominy and social decline as they age with fewer friends to even provide them some comfort.

Question 2: Does personality predict social behaviors in a dyad?

No personality factors were predictive of any of the dyad relationship styles. In humans personality factors do not necessarily predict the quality of one's relationships (Nofle & Shaver, 2006) or one's likeability (Wortman & Wood, 2011). Studies of the impact of personality on the quality of interpersonal relationships in humans have been inconsistent in their findings [see Nofle & Shaver (2006) for excellent review of these studies]. Many socially relevant items on the scale load on different personality factors, so that all personality factors have some facets that may contribute to social behavioral styles. This idea is supported by the personality subscales significance in LK analysis.

An individual's personality, as measured by re-organizing items into socially relevant subscales, was significant in the analysis of the quality of an individual's dyadic-level behaviors, but the personality factors were not. In future studies it would be prudent to utilize the factors in analysis, but not to rely solely on them to assess the true influence of personality on social behaviors.

Chimpanzees who were friendly, helpful and playful were more liked, but were not necessarily less disliked. Chimpanzees who were unpleasant, selfish, and bad-tempered did not have a lower LK score. Being a good, kind, and eminently personable chimpanzee, it seems, will produce amiable relationships, but being brutish and self-serving will not make others revile and loathe you.

Being disliked seems to be independent of personality traits in chimpanzees. It could be that being disliked is the product of a strategy that could be employed by individuals with a wide range of personality characteristics. This idea is supported by the results of the demographic GLMs as well. A high dislike score is the result of a strategy employed by males at a specific phase of their life, not an inherent personality trait. It is also possible that the relatively few number of dislike dyads reported is too small to yield significant results.

Further research is needed to distinguish between these two possibilities, perhaps by asking raters to identify dyads of chimpanzees who seem to dislike one another in a free form answer. These raters are zookeepers, and their job includes ensuring the happiness of their chimpanzees, and disliked chimpanzees are presumably not happy. The raters may be more willing to discuss dislike dyads as aberrations from their socially healthy group than to brand some dyads as disliking each other without giving them a chance to explain or qualify their answer.

There has been very little research in adult humans on the relationship between personality and likeability (Wortman & Wood, 2011). Wortman & Wood (2011) collected personality and likeability data on groups of college students (those in Greek organizations and those living in a dormitory). They found that traits across the Big 5 were correlated to likeability. Interestingly, they found items related to dominance, *e.g. bad/assertive, controlling/dominant, and forceful*, were negatively correlated to likeability, as were socially agonistic items like *jealous, devious, suspicious, manipulative, temperamental, moody, and sad/unhappy*. These items are similar to items in Agonistic domain scale in this study, which was not significant in the LK GLMs for chimpanzees. Perhaps chimpanzees are more tolerant of socially agonistic behaviors than are humans.

Wortman & Wood also found a positive correlation between socially affable items and likeability: *e.g. talkative, energetic/active, happy/joyful, cooperative, warm, and trustful*. These items are similar to the Affiliative domain scale used in the current study, which was significant correlated to LK in the GLM. Socially Affable characteristics predict likeability in both species, but socially agonistic characteristics only predicted low likeability in humans. The Wortman & Wood study stands as one of the very few to directly link personality and general likeability in human adults, but given the contrasts between our findings in chimpanzees and their findings in humans, this is an area of research that should be explored more fully.

Question 3: Does SWB predict social behaviors in a dyad?

Individuals in negative social relationships (DK) were described as neither happier nor unhappier than those who were not in negative social relationships. Likewise, individuals who were high in NT were not significantly happier or unhappier. It seems surprising that happiness is not a function of social relationships in chimpanzees, especially given the importance of social

relationship quality in human happiness (Menta & Gosling, 2008). It seems that happiness in chimpanzees is far less dependent on the quality of an individual's social life, perhaps as a result of some qualitative difference in the role or experience of relationships between our closest kin and us. This could be an area of future research in both SWB and social relationships in chimpanzees.

Follow-up question: What is NT?

If one were to attempt to design an unsuccessful chimpanzee, the NT syndrome would be an excellent starting point. Chimpanzees high in NT are: 1) not interacting with others, 2) feel insecure and impotent to control their environment, 3) un-personable and unpleasant to be around, and 4) lack the intelligence or social acumen to affect their plight.

This suite of characteristics does not simply describe a miserable, lonely chimpanzee. These traits feed upon one another to exacerbate social isolation and prevent behavioral adjustment. A chimpanzee may be alone because it is low ranking, but if it is a likeable enough chimpanzee to form bonds and savvy enough to establish alliances, it can change its social situation. A chimpanzee may be un-personable and disagreeable, but smart in making social alliances and/or high in rank. Moreover, being unpleasant does not mean one is unhappy.

The chimpanzees identified as high NT not only lack social position but also the confidence, demeanor or basic social skills to establish themselves as a part of their society. Even if they could alter some aspect of the syndrome, another would work against them and reinforce the socially maladjusted behaviors. For example, if a chimpanzee could change its demeanor and could begin to behave in a loving, affectionate manner and exhibit a playful nature, it would also have to overcome a tendency towards avoiding social situations, anxiety, potentially being ignored by others, and its own bumbling attempts at interpreting and predicting

the moods and behaviors of other chimpanzees. Likewise, if such a chimpanzee could rise in rank (say by brute force), it would still shun social interaction and likely be avoided, it would not be able to establish nurturing, supportive alliances with other males or be able to deduce the political intentions of the other chimpanzees. Each domain of the syndrome inhibits change in the other domains, dooming these chimpanzees to languish alone, confused, and unhappy as non-entities in their own troop.

Limitations of the LK, DK, NT measure

In restricting our measure of social behavior to one broad quality of dyads (like, dislike or indifferent/neutral), we of course lost much detail and nuance in the nature of individuals' interactions with one another. Now that it has been established that dyadic-level behavior in chimpanzees has a basis in some aspects of personality and demographic factors, a more focused study can be designed. Keeping in mind at all times the particular nature of conducting research with zoos and keepers, the more focused a study one can design, the more likely one is to find willing participants, we must again design the briefest measures possible to achieve our ends.

Future Directions and Analyses

Study 1. Small sample sizes made it difficult to draw any definite conclusions in the first study. A larger sample must be used: that includes more chimpanzees and more raters. The practicalities of working with zoo populations limits both the number of chimpanzees and the number of available raters; however, a large database already exists of personality and SWB data collected over the last 20 years. A study specifically targeting chimpanzees that are part of this database could yield a much larger number of chimpanzees. At any given time, the number of raters that are available to participate in these surveys is limited by the size of the zoo staff and

the time constraints on the keepers whose primary responsibility is always to the well-being of their chimpanzees. It may take several years for such a study to collect the required data.

Future research with captive zoo chimpanzees could retain the modified Round Robin design, but expand the items for each dyad from categorizing them as LK, DK, or NT. Other options could include rating the stability of the relationship (do they nearly always get along, or do they get along, but with fairly regular dust-ups). Dyads could also be measured on the level of affection (within LK dyads). In the comments sections on these surveys, or simply written into the margins of the measure itself, as well as in personal communications and informal interviews several raters indicated dyads that seemed particularly fond of each other or seemed to truly enjoy each others' company. In the 2003 study, raters also included similar comments. These types of questions would be targeted at certain types of dyads, rather than measuring a continuous variable across all dyads.

Expanding dyad attributes measured. In the last decade, monumental strides have been made in the statistical analysis of interdependent data, especially in dyads (Kenny, Kashy, & Cook, 2006). Another area of future research could exploit these advances. Using the modified Round Robin design, raters could be asked to rate the same dyad, but focusing on the different experience of each individual. For example, in this study, raters were asked if Bahati and Mollie liked, disliked, or were indifferent towards one another, producing a single score for the dyad. Raters could also be asked if Bahati liked, disliked, or is indifferent towards Mollie and if Mollie likes, dislikes, or is indifferent towards Bahati, thereby identifying groups with one-sided relationships.

Physical Well-Being, personality SWB, and relationship qualities. In humans, personality, happiness, and relationship quality all have implications for an individual's health

and lifespan. (Veenhoven, 2008) In non-humans this has been far less intensely studied, but there is evidence that this is an important, growing field of research (Alberts, 2010; Menta & Gosling, 2008). In orangutans, happiness (SWB) predicts longevity (Weiss, Adams, & King, 2011). In baboons, females with strong and consistent bonds with another female live longer, independent of the effects of rank or maternal kin (Silk, Beshner, Bergman, Crockford, Engh, Moscovice, Wittig, & Seyfarth, 2010). With a dataset of personality, SWB, demographics and relationship quality one could assess the influence of these factors on chimpanzees' physical well-being. Zoos that may be reticent to share detailed information about the medical history of their chimpanzees would be more likely to participate in research using more general, impressionistic surveys. Surveys would provide information about chimpanzee health while maintaining the privacy of zoos. Being able to predict potential health problems from measures like personality and SWB could help zoo staff tailor medical protocols to individuals' needs.

Section V: Conclusion

Conclusion

Study 1

- * Dominance rank is relatively stable in zoo populations across a ten year span.
- * Dominance Factor scores were significantly correlated between both time points.

Study 2

- * Female chimpanzees were less liked and more disliked than male chimpanzees.
- * Male and female relationship quality depended on different demographic variables. Females became less liked and more disliked as they aged. Both a male's age and his rank impacted his likeability and dis-likeability. Low ranking males were both less liked and more disliked than higher-ranking males.
- * None of the personality factors predicted scores of likeability or dis-likeability.
- * Personality items organized by an Affable and Agonistic domain show high internal consistency (alpha scores) and predict social behavior.
- * An affable personality predicted a low neutral dyad score. An agonistic personality predicted a higher neutral dyad score.
- * SWB was not related to the quality of one's social life as measured by dyad quality.
- * Rank was highly stable across 10 years.
- * Individuals with many neutral/indifferent dyads demonstrate a social maladjustment syndrome characterized by: 1) infrequent social activity, 2) insecurity and a lack of control, 3) unpersonable social interactions, 4) lack of social acumen.

Personality factor scores are not a good measure of social behavior in dyads. However, while personality factors and SWB were not significant predictors of dyadic-level behavior,

personality facets of positive and negative sociality were significant predictors of likeability. This demonstrates the overall validity of the personality scores.

There were some striking sex differences. Females tended to have less extreme social interactions and, while males could look forward to more a more enjoyable social life after the age of 25 or so, females' social lives would steadily decline in pleasantness. Finally, there appears to be a behavioral syndrome of social ineptitude and avoidance in chimpanzees.

There is something driving the nature and tenor of chimpanzee social interactions that is more than any given individual's personality, age or even rank. This study has begun to illuminate some traits that contribute to relationship qualities in chimpanzees, but further study is called for to understand individual differences in chimpanzee social behavior. More broadly, this area of research will provide insight into human behavior, SWB, and the importance of social relationships. Any differences in the relationships between friendship, SWB, and personality comparing chimpanzees and humans may be indications of different evolutionary pressures our respective ancestors experienced and the adaptations they evolved in response to those pressures.

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Table 1. Personality Factors and items that loaded on the Factors

Factor	Items
Dominance Factor	Dominant, Independent, Intelligent, Bullying, Stingy/Greedy, Submissive (-), Fearful (-), Timid (-)
Extraversion Factor	Active, Sociable, Friendly, Affectionate, Solitary (-)
Dependability	Predictable, Impulsive (-), Reckless (-), Jealous (-)
Agreeableness	Sympathetic, Sensitive, Helpful, Protective, Gentle
Emotional Stability	Stable, Excitable (-)
Openness	Inquisitive

Table 2. Personality domains and items used in domain scales

Domain	Items
Affable	Friendly, Affectionate, Sympathetic, Helpful, Protective, Gentle, Loyal, Popular, Loving/Caring, Cooperative, Playful: Other-focused
Agonistic	Bullying, Stingy/Greedy, Jealous, Fickle, Hostile, Devious/Calculating

Table 3. Demographics for each zoo

Zoo	Number of Chimpanzees	Number of raters	Average Age of Chimps	Average time raters had known chimps
1	7 M=3 F=4	5	M=20.68 SD=4.32	M=13.5 SD=7.64
2	6 M=3 F=3	5	M=27.76 SD=15.86	M=7.77 SD=7.52
3	9 M=5 F=4	8	M=31.41 SD=10.57	M=9.38 SD=7.96
4	8 M=2 F=6	7	M=18.94 SD=10.40	M=7.31 SD=2.50
5	9 M=2 F=7	5	M=21.70 SD=11.10	M=5.96 SD=2.86
6	19 M=6 F=13	5	M=30.47 SD=15.85	M=7.46 SD=10.71
7	12 M=4	7	M=26.42 SD=13.37	M=6.63 SD=2.81

	F=8			
8	6 M=4 F=2	2	M=20.70 SD=12.03	M=9.08 SD=6.33
9	3 M=1 F=2		M=45.43 SD=9.93	M=4.67 SD= 2.18
10	6 M=2 F=4		M=20.09 SD=5.37	M=4.67 SD=2.11

Table 4.1. Inter-rater reliabilities for 2012-2013 data: Dominance Factor.

Zoo	Mean number of chimpanzees	Mean number of raters	ICC (3, <i>k</i>)	ICC (3,1)
1	6	4	0.8963	0.6733
2	3	2.875	0.9424	0.8501
3	8	2	0.8248	0.7012
4	8.8	4.89	0.9621	0.8384
5	18.83	5.89	0.8852	0.5669
6	10	5	0.9189	0.6939
7	2	3	0.9493	0.8619
8	5	3	0.9225	0.7954
9	3	3	-1.6152	-0.2593
10	6	3	0.9346	0.6946

Table 4.2. Inter-rater reliabilities for 2012-2013 data: Extraversion Factor.

Zoo	Mean number of chimpanzees	Mean number of raters	ICC (3, <i>k</i>)	ICC (3,1)
1	6	4	0.8353	0.5417
2	8	3	-0.4671	-0.1187
3	8	2	0.6180	0.4471
4	8.8	4.89	0.8817	0.6039
5	18.83	5.95	0.5197	0.1539
6	10	5	0.7899	0.4426
7	2	3	0.9342	0.4469
8	5	3	0.8390	.6346
9	3	3	0.5483	0.2281
10	6	3	0.7031	0.4412

Table 4.3. Inter-rater reliabilities for 2012-2013 data: Dependability.

Zoo	Mean number of chimpanzees	Mean number of raters	ICC (3, <i>k</i>)	ICC (3,1)
1	6	4	0.9246	0.7540
2	8	3	-0.0584	-0.0187
3	8	2	0.7088	0.5490
4	8.8	4.89	0.9134	0.6899
5	18.83	5.95	0.7456	0.3300
6	10	5	0.8023	0.4480
7	2	3	0.7456	0.4941
8	5	3	0.3791	0.1691
9	3	5	0.7258	0.3461
10	6	3	0.6614	0.3943

Table 4.4. Inter-rater reliabilities for 2012-2013 data: Agreeableness Factor.

Zoo	Mean number of chimpanzees	Mean number of raters	ICC (3, <i>k</i>)	ICC (3,1)
1	6	4	0.7359	0.4106
2	8	3	-0.3415	-0.0927
3	8	2	0.2697	0.1585
4	8.8	4.89	0.2186	0.0541
5	18.83	5.95	0.6968	0.2787
6	10	5	0.7726	0.4046
7	2	3	0.9183	0.7894
8	5	3	0.7271	0.4602
9	3	3	0.8747	0.6994
10	6	3	0.4101	0.1860

Table 4.5. Inter-rater reliabilities for 2012-2013 data: Emotional Stability Factor.

Zoo	Mean number of chimpanzees	Mean number of raters	ICC (3, <i>k</i>)	ICC (3,1)
1	6	4	0.6420	0.3180
2	8	3	-0.1819	-0.0541
3	8	2	0.8353	0.7168
4	9	5	0.8096	0.5498
5	19	6	0.7004	0.2803
6	10	5	0.8032	0.4454
7	2	3	-0.3333	-0.0909
8	5	3	0.8154	0.5955
9	3	3	0.8503	0.6544
10	6	3	0.7886	0.5542

Table 4.6. Inter-rater reliabilities for 2012-2013 data: SWB.

Zoo	Mean number of chimpanzees	Mean number of raters	ICC (3, <i>k</i>)	ICC (3,1)
1	6	4	0.8063	0.5100
2	8	3	0.6719	0.4056
3	8	2	-2.314	-0.5364
4	9	5	0.9604	0.8290
5	18	5.68	0.6681	0.2617
6	4.9	4.9	0.8776	0.5485
7	2	3	0.8936	0.7368
8	5	3	0.9546	0.8752
9	3	3	0.6150	0.3487
10	6	3	0.2976	0.1238

Table 5. Mean Inter-rater reliabilities

Variable	ICC (3, <i>k</i>)	ICC (3,1)
Dominance Factor	M= 0.6621 SD= 0.8011	M= 0.6416 SD= 0.3303
Extraversion Factor	M= 0.7563 SD= 0.4691	M= 0.3684 SD= 0.1221
Dependability Factor	M= 0.6548 SD= 0.2926	M= 0.4156 SD= 0.2312
Agreeableness Factor	M= 0.5282 SD= 0.3910	M= 0.3349 SD= 0.2766
Emotional Stability Factor	M= 0.5730 SD= 0.4437	M= 0.3969 SD= 0.2828
SWB	M= 0.4431 SD= 0.9893	M= 0.4129 SD= 0.4125

Table 6. Correlations between 2003 and 2013 data

Variable	Correlation Coefficient	<i>N</i>	Items loading on Factors	Correlation Coefficient	<i>N</i>
Dominance rank	0.338* 0.02	45			
Dominance Factor	0.723* 0.00	23			
			Dominant	0.773* 0.000	24
			Independent	0.557* 0.006	23
			Intelligent	0.440* 0.031	24
			Bullying	0.420* 0.041	24
			Stingy/Greedy	0.300 0.154	24
			Submissive	0.447* 0.029	24
			Fearful	0.682* 0.000	24
			Timid	0.592* 0.002	24

Extraversion Factor	0.261 0.21	24			
			Active	0.263 0.214	24
			Sociable	0.319 0.129	24
			Friendly (s)	0.338 0.106	24
			Affectionate	0.094 0.662	24
			Solitary (s)	0.397 0.055	24
Dependability/ Conscientiousness Factor	0.267 0.207	23			
			Predictable	0.079 0.715	24
			Impulsive	0.154 0.472	24
			Reckless	0.492* 0.036	24
			Jealous	-0.029 0.894	24

Agreeableness Factor	0.422*	24			
	0.04				
			Sympathetic	0.151	24
				0.482	
			Sensitive	0.333	24
				0.112	
			Helpful	0.281	24
				0.184	
			Protective (s)	0.183	24
				0.393	
			Gentle	0.566*	24
				0.004	
Emotional Stability Factor	0.339	24			
	0.105				
			Stable	0.422*	24
				0.030	
			Excitable	0.015	24
				0.945	
Openness Factor	0.310	24			
	0.140				
			Inquisitive	0.310	24
				0.130	
loving/caring item	0.489	9			

	0.182				
Hostile item	0.753*	9			
	0.019				
Cooperative item	0.729*	9			
	0.026				
Socially perceptive item	0.716*	9			
	0.030				
Peacemaker item	0.457	9			
	0.216				
Happy item	0.637	9			
	0.065				
SWB	0.390*	27			
	0.044				
			Happy mood	0.092	27
				0.649	
			Satisfying social interactions	0.267	27
				0.178	
			Effective at achieving goals	0.659*	27
				0.000	
			Be chimp	0.155	27
				0.442	

Correlations are Pearson's r correlation coefficients.

Figure 1. Male and Female LK scores (number of *like* dyads/number of reported relationships) across age groups

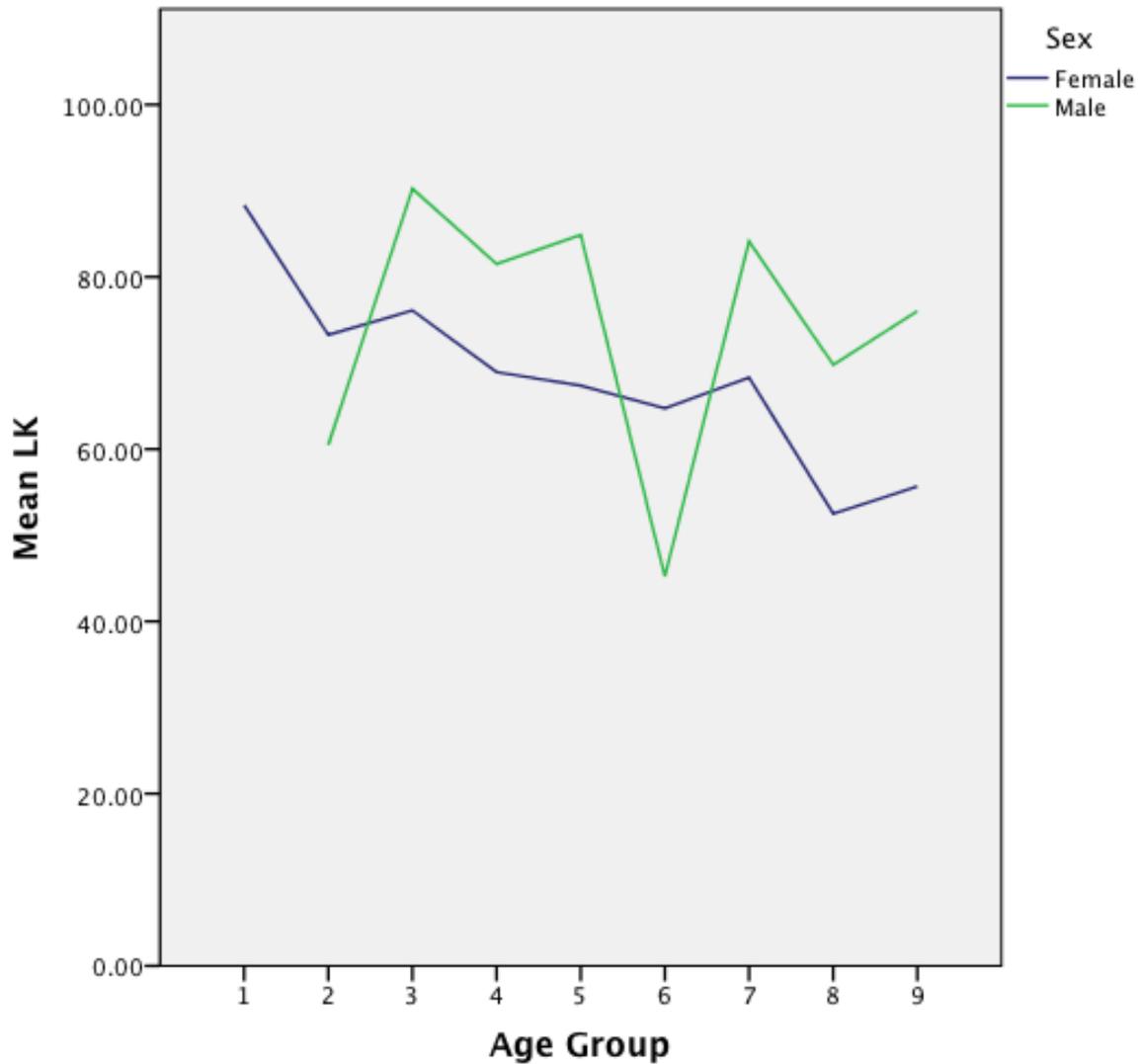


Figure 1. Mean LK score (number of *like* dyads/number of reported relationships) across age groups: 1=age 5 to 10 years of age (N=2), 2=10.01 to 15 years of age (N=19), 3=15.01-20 years of age (N=10), 4=20.01 to 25 years of age (N=9), 5=25.01 to 30 years of age (N=6), 6=30.01 to 35 years of age (N=5), 7=35.01 to 40 years of age (N=6), 8=40.01 to 45 years of age (N=11), 9=45.01 years of age or older (N=6)

Figure 2. Male and Female DK scores (number of *dislike* dyads/number of reported relationships) across age groups

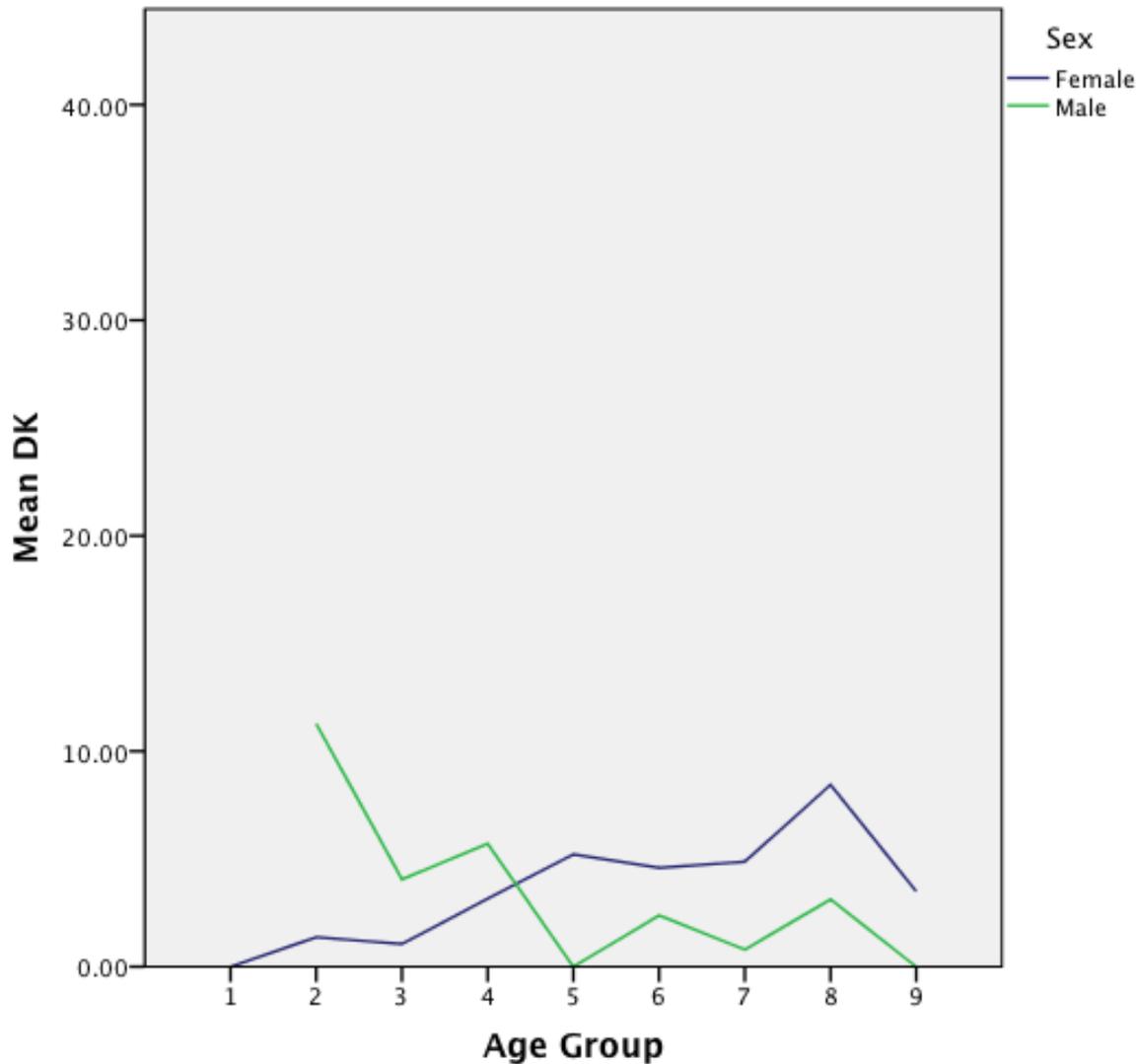


Figure 2. Male and Female DK scores (number of *dislike* dyads/number of reported relationships) across age groups: 1=age 5 to 10 years of age (N=2), 2=10.01 to 15 years of age (N=19), 3=15.01-20 years of age (N=10), 4=20.01 to 25 years of age (N=9), 5=25.01 to 30 years of age (N=6), 6=30.01 to 35 years of age (N=5), 7=35.01 to 40 years of age (N=6), 8=40.01 to 45 years of age (N=11), 9=45.01 years of age or older (N=6)