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Determining Personality in Sanctuary Chimpanzees (*Pan troglodytes*)

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INTRODUCTION

Why Research Personality?

Human personality research has been ongoing for decades. The importance of individual differences (i.e. personality) within human social relationships has been acknowledged by many disciplines (Dutton, Clark, & Dickens, 1997). The insight that can be gained from personality research extends far beyond that of human social relationships. Personality research can provide information about: an individual's subjective well-being (Weiss, King, & Perkins, 2006; King & Landau, 2003), the heritability of behavior traits (Weiss, King, & Figueredo, 2000), the evolutionary nature and origins of personality (Gosling & John, 1999, Uher, 2008), the prediction of future behavior (Capitano, 1999; Gosling & Vazire, 2002; Pederson, King, & Landau, 2005) or even predicting one's physiological capability to respond to infectious disease (Capitano, Mendoza, & Baroncelli, 1999). Personality is not limited to humans, as individual personality is well noted in many species including nonhuman primates, many other mammals, and even octopuses and guppies (Gosling & John, 1999). Researching animal personality for comparison can be beneficial in many ways. By comparing human personality research with research on other animals, any commonalities and/or differences that emerge will inform us about what humans are and are not as a species. Moreover, these patterns highlight evolutionary relationships between organisms through behavior. The current study aims primarily to test the new personality assessment methodologies developed by Uher (2008) in a captive population of chimpanzees (*Pan troglodytes*). If this methodology is successful, the secondary goal of this study is to explore the role of chimpanzee personality within groups and across age and sex classes.

Human Five-Factor Model

The Five-Factor Model originally developed in psychology as a method to research personality in humans. Now, these same methods are being applied to investigate personality in nonhuman animals as well. The Five-Factor Model is a hierarchical model with five broad factors or dimensions, which represent categories of personality at the broadest level. These factors or dimensions are commonly referred to as Neuroticism, Agreeableness, Extraversion, Open to Experience, and Conscientiousness. The dimensions listed above are actually bipolar constructs, and the nomenclatures listed above are just one end of each dimensional spectrum. It is important to understand both extremities of each dimension, and they may be more appropriately referred to as: Neuroticism vs. Emotional Stability (N), Agreeableness vs. Antagonism (A), Extraversion vs. Introversion (E), Open vs. Closed to Experience (O), and

Conscientiousness vs. Impulsiveness (C). In nonhuman animals there are two additional dimensions, Dominance and Activity. In humans Dominance is included in the Extraversion vs. Introversion dimension. For animals, Dominance has more diverse personality implications than in humans, and is therefore classified as its own dimension, a sixth factor in the human Five-Factor Model (Gosling & John, 1999). In both humans and nonhumans, Activity is coupled to age. In adults Activity is integrated with the Extraversion vs. Introversion dimension, whereas in juveniles Activity is treated as a separate dimension (Gosling & John, 1999). The current study does not have any adolescent subjects and therefore does not treat Activity as a separate factor. For clarification, this study will use Dominance as an additional dimension to the human Five-Factor Model.

Within each of these dimensions are several *facets*, specifying the *dimensions* and forming the first sublevel of this hierarchal model. The following are examples of the facets in each dimension outlined by Gosling & John (1999):

- Neuroticism vs. Emotional Stability (anxiety, depression, vulnerability to stress, moodiness)
- Agreeableness vs. Antagonism (trust, tender mindedness, cooperation, lack of aggression)
- Extraversion vs. Introversion (sociability, assertiveness, activity, positive emotions)
- Open vs. Closed to Experience (ideas/intellect, imagination, creativity, curiosity)
- Conscientiousness vs. Impulsiveness (deliberation, self-discipline, dutifulness, order)

The next subsets of the hierarchy are the *specific traits* that describe each *facet*. These descriptors may vary from study to study depending on the aims of the study and the species being studied. For example, one *specific trait* used in the “sociability” *facet* might be a “talkative” descriptor; that is, how talkative one is may be a possible indicator of how social one is. Of course, there are multiple *specific traits* for each *facet*. Therefore, the “sociability” of an individual would not be measured solely on how “talkative” the individual is, but how “talkative” one is may be used in conjunction with other *specific traits* to measure how “sociable” the individual is.

Subjective Well-Being

Subjective well-being, also known in psychology as “happiness,” has been studied in both humans and other animals. In humans, it has been suggested that subjective well-being in the long-term is minimally affected by external factors (Lykken & Tellegen, 1996). A study of 1,155 sets of human twins by Lykken & Tellegen (1996) showed that individual subjective well-being could not be influenced by differences in socioeconomic status, educational attainment, family income, marital status, sex, or religious commitment. Instead, this study found that the stable component of individual well-being was genetic variation. What this study did not address however, is that personality traits may be heritable. Interestingly, another investigation of this concept suggested that personality is accounting for most of the variation in human subjective well-being (Costa

& McCrae, 1980). Costa and McCrae (1980) explain specifically that subjective well-being is positively correlated with the Extraversion personality dimension and negatively correlated with the Neurotic dimension. Similar results have been produced in animal populations.

In zoo-kept orangutans, Weiss, King, and Perkins (2006) found that when orangutan personality was correlated with their subjective well-being, Extraversion and Agreeableness dimensions associated positively with “happiness”, while Neuroticism had a negative association. The similarity between humans and their closest living relatives are strikingly similar. Chimpanzees (*Pan troglodytes*) were assessed by King and Landau (2003) across thirteen different captive environments. Again, results showed no major differences in the relationship between subjective well-being and personality when compared with human studies (King & Landau, 2003). These studies illustrate that personality identification is of great importance in assessing the subjective well-being of an individual in not only human populations but across different species. These personality studies also show some of the dimensional commonalities found between apes and humans. Subjective well-being is important to humans for obvious reasons, but is also becoming increasingly important to nonhuman primates. With growing populations of animals in zoos and sanctuaries, rehabilitation and breeding programs, and in laboratories, a concern with animal treatment and subjective well-being is also escalating.

Heritability

The five broad-spectrum personality dimensions that have emerged from human personality research, account for most of the variation within populations. These five factors have repeatedly been found throughout both Western and non-Western societies regardless of language and cultural differences (Weiss, King, & Figueredo, 2000). This suggests that personality dimensions may share a biological foundation and, moreover, may not be limited to humans (Weiss, King, & Figueredo, 2000). If personality has a biological basis then, theoretically, personality traits should be heritable. Indeed there are substantive findings showing that some personality traits are heritable. For example, Hansen’s (1996) research demonstrated that it is possible to select for “fearfulness” in minks (as cited in Gosling & Vazire, 2002). Another example is a heritability analysis that was performed on captive chimpanzees from twelve different locations (Weiss, King, and Figueredo, 2000). In these studies, chimpanzee personality factors were measured for broad-sense heritability and narrow-sense heritability. Broad-sense heritability is an estimate of variance due to additive and non-additive genetic effects, whereas narrow-sense heritability is an estimate of variance due to additive genetic effects only. Weiss, King, and Figueredo (2000) found that Dominance was significantly heritable in chimpanzees. There was some insignificant evidence of Dependability (Conscientiousness) traits being heritable, although even less significant Agreeableness and Emotional Stability traits showed a positive correlation with heritability (Weiss, King, & Figueredo, 2000).

Another more common application of the concept of personality being heritable is selective breeding in domestic animals. Domestic animals are not only selected for preferred physiological characteristics, but for personality traits as well. For example, sheep or cows may be selected for docile behavior, while dogs may be selected for their obedience and loyalty. The result is that domestic animals are often extremely different from their wild counterparts, in both physiological and behavioral aspects.

Understanding personality is pertinent to our understanding of the heritability of behavior in all species. Further knowledge on this topic could be directly applied to humans. What if criminal tendencies are inherited? Is emotional stability inherited and if so, how? Is our overall “happiness” inherited? If this is true, Lykken and Tellegen (1996) argue that “it may be that trying to be happier is as futile as trying to be taller and therefore is counterproductive” (p. 189). In the future, biological personality research may be able to answer some of these questions. Although we do not yet completely understand the heritability of personality, it is clear that they are somehow linked. To assess the heritability of personality is difficult because to a degree, the environment also plays a role.

Personality: Evolution and Origins

When thinking about selection pressures (natural or sexual), we tend to think that our direct fitness level is affected by phenotypic traits, but generally these traits only come from anatomical, morphological, and physiological perspectives. “Yet there is nothing in evolutionary theory to suggest that only physical traits are subject to selection pressures” (Gosling & John, 1999, p. 69). And personality is exactly that, a dynamic phenotypic trait that directly affects one's fitness level. Weiss, King, & Perkins (2006) explain that this idea “...can be traced back to Darwin (1998/1872), who noted that mental faculties were subject to natural selection, and to his contemporaries (e.g., Hobhouse, 1901; Romanes, 1884), who speculated about the evolution of mind, intelligence, and consciousness in a variety of nonhuman species” (p. 501). For instance, the reproductive success of an individual can be impacted negatively by chronic states of anxiety, and is therefore linked to an individual's tenseness and fearfulness (Gosling & Vazire, 2002). In cheetahs, Wielebnowski (1999) used tenseness and fearfulness to accurately predict breeding patterns, and found that non-breeding cheetahs were rated higher in these categories (as cited in Gosling & Vazire, 2002). These are just two examples of natural selection pressures, but what about sexual selection pressures? Are certain personality traits desired more than others when choosing a mate? In humans, personality can be one of the largest single factors when choosing a significant other. Animals exhibit preference for personality traits as well. For instance, if a female gorilla is selecting for the male that has the most potential for providing safety for her and her offspring, she is not only selecting for the size of the male, but also any dominance and/or aggressiveness exhibited by the male. Just because a male is large does not mean that he will fight, which indicates that individual personality may play a larger role in evolution than we previously thought.

Uher (2008) argues that because personality leads to behavior that is dynamic and diverse, individual responses to the environment should lead to neurological and

morphological refinements; and these small outputs could trigger diversification. This is suggesting that behavior is an evolutionary motor rather than a byproduct from evolutionary processes. In further support, Pederson, King, & Landau (2005) state that the variation in personality is relatively large when compared to other types of phenotypic variation, and that this may reflect the adaptive value of personality. It has even been argued that "...the most direct route through which personality traits can contribute to individual differences in fitness is through personality linkages with behavior" (Pederson, King, & Landau, 2005.)

The origins of personality are still unclear; however cross-species examinations have identified a few common personality dimensions that may have served as adaptive functions (Dutton, 2008). Cross-species comparisons are important because each species is likely to have different phylogenies, ecologies, social systems, etc. Any commonality emerging regardless of these variables may give insight to evolutionary mechanisms and processes (Uher, 2008). It is also believed that the biological foundation of personality preceded the emergence of modern humans (Weiss, King, & Figueiredo, 2000). Humans and chimpanzees share a common ancestor, and this personality relationship is evident because humans exhibit five personality dimensions, and chimpanzee personality comprises of these same five dimensions, plus an extra dimension called Dominance. So when did Dominance appear in chimpanzees? Did it appear in chimpanzees after they speciated? Did humans lose this trait after speciation? Or was it a driving force for the speciation of humans and chimpanzees? Another commonality between chimpanzee and human personality is to date, they are the only two species to exhibit a Conscientiousness factor. Does this suggest that Conscientiousness evolved in the human/chimpanzee lineage? A personality study on orangutans resulted in a clear absence of Conscientiousness, but the author argues that this does not mean the dimension is not there, but that it may be exhibited at different levels in orangutans than in chimpanzees and humans (Weiss, King, & Perkins, 2006). Regardless, more research needs to be conducted before these types of questions can be answered with any validity. Although there are no definitive answers, it is clear that individual personality plays a vital role in our evolutionary past and future.

Predicting Future Behavior

It is thought that knowledge of an individual's personality can aid in predicting that individual's future behavior. Pederson, King, & Landau (2005) found in captive zoo-housed chimpanzees that those chimpanzees labeled as Dominant and Emotional were performing more agonistic behaviors, whereas the chimpanzees categorized as Dependable and Agreeable were demonstrating significantly less agonistic behaviors. Moreover, those with Extraverted and Affinitive personalities exhibited higher levels of activity (gymnastics) and positive social behaviors (Pederson, King, & Landau, 2005). Activity and Extraverted/Affinitive personality has paralleled in human populations. Pederson et al. (2005) states that "...chimpanzees who frequently use ropes, artificial trees, and climbing structures for vigorous gymnastic activity and humans who frequent jogging courses and fitness gyms may share an abundant amount of a common personality trait, namely Extraversion" (p. 545).

Another study on rhesus macaques experimented with the ability of personality to predict behavior in different situations (Capitanio, 1999). In this study baseline personality was scored on each subject, and then the subjects were presented with a threatening human, stable and unstable group, videotapes of social behavior, and social dyads. Results from this study indicated substantial predictability for many different combinations of personality and situations. Although there is a paucity of research on the ability of personality to predict future behavior, it is nonetheless important because it opens an area of research to test the accuracy of personality predicting future behavior, such as the formation of new chimpanzee social groups.

Response to Disease

Another major reason that personality studies are important is that there is evidence that personality can affect one's ability to respond to infectious disease. Capitanio, Mendoza, and Baroncelli (1999) investigated the role of personality to individual responses to disease. During this study, adult rhesus macaques were assessed for personality using similar techniques to those used for human personality research. Individual personality was assessed while the monkeys were living in their natal groups. This provided a baseline data for each individual's personality. Roughly eighteen months later, the macaques were inoculated with a simian immunodeficiency virus (SIV). From here the monkeys were exposed to both stable and unstable environments. Next, at regular intervals, the researchers recorded the IgG response to SIV, the IgG response to rhesus cytomegalovirus, the viral load, and behavior. This study found that after inoculation, the "Sociable" individuals showed better responses to plasma cortisol concentrations, anti-RhCMV IgG, and SIV RNA. These results underscore the potential control that personality may have over physiological processes. Although it is not certain, if personality plays a vital role in individual responses to infectious diseases, how would the change the way we practice Western medicine?

Traditional Methods

To date, traditional methods used for assessment of individual personality in nonhuman animals have included surveys from animal keepers and care staff. Generally, animals are scored for presence or absence of personality traits on a scale, using the human Five Factor Model. This subjective approach limits the scientific value for several reasons. For instance, the traits and scales used in these surveys often vary from one study to the next, making it difficult to directly compare results across studies. Some keepers may know specific animals better than others which may lead to stronger inter-observer variation. Others might be judging animals based on first impressions that are not representative of the animal's true personality. Animals may also be "pigeon-holed", meaning that a rater does not know the subject animal yet; the rater only knows another person's opinion about the animal's personality. Any predisposition to an animal's personality can influence what the rater sees, creating a bias, and ultimately "pigeon-holing" the animal. Furthermore, keepers and care staff impressions are generally measured from personal interactions with the animals. However, animals may act differently toward their

conspecifics than toward humans, and measuring these interactions should be equally if not more important. These problems were evident in few studies. Bolig, Price, O'Neill, & Suomi (1992) found poor inter-observer agreement in their study on rhesus macaque personality. Furthermore, another study on rhesus macaques by Martau, Caine, and Candland (1985) had poor inter-observer reliability based on the observer's experience level and in macaques undergoing status changes. Further yet, Martin (2005) noticed that rearing strategy was a circumstantial function of rater reliability. In this study captive chimpanzees that were human-reared were rated less reliably than those chimpanzees that were mother-reared. For humans these traditional techniques hold more validity because the subject can be surveyed directly. Conversely, because animals cannot complete a survey themselves, a keeper or care staff member is augmented to complete it for them limiting its validity. Moreover, traditional methods are problematic because they are generally not comparable. It is important to establish methods that can be used uniformly for comparison, because comparative personality research is stretched across many disciplines including: animal personality psychology, anthropology, behavioral ecology, behavior genetics, cross-cultural psychology, evolutionary biology, human personality psychology, evolutionary psychology, neurosciences, theoretical biology, veterinary sciences, and zoology. Because there is a diverse spectrum of disciplines focusing on comparative personality research, an overarching methodological framework is missing.

New Methods

In contrast to the problematic survey assessment method, Uher (2008) proposed a new methodological framework for comparative personality research that is derived from the subject species' behavioral repertoire, and is approached from the "bottom-up". The "bottom-up" approach, instead of subjectively surveying individuals for dimensional factors of personality from the top-down, is objectively scored based on observed behaviors or *specific traits* from the bottom-up, because complete dimensions of personality are not directly observable but individual behaviors that comprise the dimension are. Uher (2008) argues that, observing from the bottom-up should allow us to quantify personality in individuals. A factor analysis of the observed behaviors should highlight any significant personality dimensions in individuals. Comparing these results should then reveal any personality differences between individuals. Essentially, it is the process of measuring personality traits for an individual, pulling out any significant personality traits through a factor analysis, and building a "personality profile" based on the personality dimensions that emerge.

The next step is to analyze individuals for comparability, uniqueness, and universality (Uher, 2008). The basic unit of analysis in comparative personality research is the individual. Individuals within studies can be compared to find commonalities, contrasted to find uniqueness, and compared with baseline data from a reference population for universality. It is important analyze individuals in all three of these viewpoints because it exhibits any intraspecific variation. To date, our understanding of nonhuman social behaviors have focused on commonalities within species known as "species-specific" or "species typical" behaviors. Any idiosyncrasies or deviance from "normal" behaviors

were generally discarded or seen as outliers (Dutton, Clark, & Dickens, 1997). As a consequence, we know little about variation within nonhuman populations.

For comparative personality researchers, the new “behavioral repertoire bottom-up” approach (Uher, 2008) should be a useful tool for comparing research across disciplines, and to minimize bias by bottom-up objective methods vs. the traditional subjective methods. Moreover, this should allow researchers to explore the extreme variation within species that has been traditionally overlooked and discarded, especially in animals. Chimpanzees are said to be everything from “good and ill-natured individuals, stable and unstable, calm and excitable, industrious and lazy” (Yerkes, 1939, p. 112).

Aims of this Study

The primary goal of this study is to test Uher’s (2008) “bottom-up” method in the assessment of personality in a captive population of chimpanzees (*Pan troglodytes*). We made a modification to these personality assessment methods. We do not have the opportunity to perform any experiments with our subject population. Consequently, we are aiming to test these methods through behavioral observations only. On that note, we do not expect to capture the Conscientiousness dimension as this factor is difficult to confine through observations alone. Theoretically, the rest of the personality dimensions being measured should manifest without experimentation. If these methods work by emphasizing intra-specific variation in personality, a secondary aim of this study is to explore the role of personality across age and sex classes, and within the group.

METHODS

Sample

This study was carried out with a group of captive chimpanzees who reside at Chimp Haven, Inc., the National Chimpanzee Sanctuary. These chimpanzees come from various backgrounds including: biomedical research, the pet trade, the entertainment industry, and rescues. Chimp Haven, Inc. currently houses 128 chimpanzees in group sizes ranging from 3 to 19. The chimpanzees have unlimited access to various environments including play yards, courtyards, 5 acre habitats, and enclosed bedrooms. Some of these areas are considered “out of sight”, and because of this we chose a subject group based on the best visual access instead of group size and age demographics. Despite these limitations, our subject group (Hamlet’s group) initially consisted of 14 individuals (7 male and 7 females) ranging in ages from 24 to 49. Over the course of the study, one male (Floyd) passed away and was removed from our study.

Site

Chimp Haven Inc. is located on over 200 acres in the remote area of Keithville, Louisiana. Chimp Haven Inc. was founded in 1995 with a mission to “...design,

construct, and manage humane, cost effective social housing for government-owned and other unwanted chimpanzees” (from their website).

Data Collection

Data were collected using continuous focal sampling methods (Altmann, 1974). This is where the observer records all behaviors seen in an individual (focal) animal over a specific amount of time. Observation sessions were completed in 10 minute increments. Data were recorded directly into a laptop computer containing observational software (The Observer[®]XT 9.0 by Noldus). Data were collected from June 22, 2009 to July 24, 2009.

Ethogram

An ethogram is a list of discrete behaviors that are common to all members of a species. The ethogram we established for this study was compiled from other ethograms on both captive and wild chimpanzee populations. Our final ethogram resulted in a total of 79 behaviors.

Assumptions

There are a few assumptions that may or may not limit our methodological approach. This study assumes that the gerontological theory of Personality Continuity is valid (Atchley, 1989). Personality Continuity theory argues that an individual’s personality remains relatively constant throughout time and across contexts (social, environmental, etc.). Although this study cannot directly test the validity of this theory, it can provide a baseline dataset. In the future, if these same individuals are re-sampled, in a different temporal context, the new data could be compared with the baseline data to reveal any theoretical validity. Akin to this, if these same individuals were re-sampled in different group contexts it could again be compared.

RESULTS

A factor analysis was performed on our dataset to highlight behaviors that load together. The aim was to find behaviors (for each individual) that would group together, and see if any of these factors corresponded to behaviors typically within any of the six personality dimensions. After this, the goal was to see which personality dimensions were prevalent for each individual, also known as building a ‘personality profile’.

The factor analysis resulted in eight groups of behaviors with significant correlations. Six of these groups were unrelated behaviors factored as belonging together, and are thus largely irrelevant. The other two groups exhibited related behaviors. The first was a group of three behaviors that are all typical of the dimension Dominance, found in nonhuman animals, with a weak correlation but nonetheless relevant in respect to the

ratio of individuals to scored behaviors (Chronbach's Alpha 0.638). Conversely, this group factor was limited to three behaviors, and Dominance cannot necessarily be undoubtedly represented by these three behaviors. The second group of related behaviors consisted of four vocalizations. Each of these vocalizations is semantically different. Therefore this factor does not reveal any particular personality dimension, just that some individuals are significantly more vocal than others (Chronbach's Alpha 0.696).

Because dimension-specific behaviors did not group together, our results are essentially inconclusive. We were not able to build 'personality profiles' without evidence of personality dimensions. One major problem was that the ratio of behaviors to individual chimpanzees (79:13) was too high. To correct for this error, behaviors were grouped into larger categories, which produced our findings, but the ratio was still inappropriate for factor analyses.

DISCUSSION

In the future, we would definitely adjust our protocol. First, an appropriate sample size is crucial to the significance of any data, and, in this case, is also relative to the number of behaviors it is loaded against (when factor analyses is the preferred statistical test). Therefore, we would seek to increase our sample size and reduce the number of scored behaviors, better meeting the basic requirements of factor analysis. Second, random sampling is important for achieving data that is representative of the group. While both of these issues were accounted for in our initial project proposal, limitations within the host facility prevented both a larger sample size and fully random observations. Because this project was preliminary, we decided to press on regardless of these restrictions. The final thing we would do differently was not accounted for in our proposal. We should have researched the basic assumptions required for factor analysis more completely, and formatted our data accordingly prior to collection. In this case, we knew we needed a factor analysis, but were unaware that the ratio of individuals sampled to the number of scored behaviors would be problematic in analysis. Had we known this ahead of time, we could have formatted our data collection and constructed our ethogram differently.

Standardized methods for objectively quantifying personality are still being developed in nonhuman personality research. It is, however, commonly accepted across several disciplines that nonhuman animals do have individual personalities that could be quantified. We feel confident that, even though we have yet to find a means of accurately scoring personality in nonhuman animals, appropriate methods will eventually be developed. Hopefully future researchers interested in developing personality assessment methodologies can learn from this preliminary study through both its strengths and weaknesses.

References

- Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behavior*, 49(3/4), 227-267.
- Atchley, R. C. (1989) A continuity theory of normal aging. *The Gerontologist*, 29(2), 183-190.
- Bolig, R., Price, C. S., O'Neill, P. L., & Suomi, S. J. (1992). Subjective assessment of reactivity level and personality traits of rhesus monkeys. *International Journal of Primatology*, 13(3), 287-306.
- Capitano, J. P. (1999). Personality dimensions in adult male rhesus macaques: Prediction of behaviors across time and situation. *American Journal of Primatology*, 47, 299-320.
- Capitano, J. P., Mendoza, S. P., & Baroncelli, S. (1999). The relationship of personality dimensions in adult male rhesus macaques to progression of simian immunodeficiency virus disease. *Brain, Behavior, and Immunity*, 13, 138-154.
- Costa, P. T., & McCrae, R. R. (1980). Influence of extraversion and neuroticism on subjective well-being: Happy and unhappy people. *Journal of Personality and Social Psychology*, 38(4), 668-678.
- Dingemanse, N. J., & Reale, D. (2005). Natural selection and animal personality. *Behaviour*, 142, 1165-1190.
- Dutton, D. M. (2008). Subjective assessment of chimpanzee (*Pan troglodytes*) personality: reliability and stability of trait ratings. *Primates*, 49, 253-259.
- Dutton, D. M., Clark, R. A., & Dickins, D. W. (1997). Personality in captive chimpanzees: Use of a novel rating procedure. *International Journal of Primatology*, 18(4), 539-551.
- Gosling, S. D., & John, O. P. (1999). Personality Dimensions in nonhuman animals: A cross-species review. *Current Directions in Psychological Science*, 8(3), 69-75.
- Gosling, S. D., & Vazire, S. (2002). Are we barking up the right tree? Evaluating a comparative approach to personality. *Journal of Research in Personality*, 36, 607-614.
- Itoh, K. (2002). Personality research with non-human primates: Theoretical formulation and methods. *Primates*, 43(3), 249-261.
- King, J. E., & Figueredo, A. J. (1997). The five-factor model plus dominance in chimpanzee personality. *Journal of Research in Personality*, 31, 257-271.
- King, J. E., & Landau, V. I. (2003). Can chimpanzee (*Pan troglodytes*) happiness be estimated by human raters? *Journal of Research in Personality*, 37, 1-15.
- Lykken, D., & Tellegen, A. (1996). Happiness is a stochastic phenomenon. *Psychological Science*, 7(3), 186-189.
- Martau, P. A., Caine, N. G., & Candland, D. K. (1985). Reliability of the emotions profile index, primate form, with *Papio hamadryas*, *Macaca fuscata*, and two *Saimiri* species. *Primates*, 26(4), 501-505.
- Martin, J. E. (2005). The influence of rearing on personality ratings of captive chimpanzees (*Pan troglodytes*). *Applied Animal Behavior Science*, 90, 167-181.
- Murray, L. E. (1998). The effects of group structure and rearing strategy on personality in chimpanzees *Pan troglodytes* at Chester, London ZSL and Twycross Zoos. *International Zoo Yearbook*, 36, 97-108.

- Pederson, A. K., King, J. E., & Landau, V. I. (2005). Chimpanzee (*Pan troglodytes*) personality predicts behavior. *Journal of Research in Personality, 39*, 534-549.
- Uher, J. (2008). Comparative personality research: Methodological approaches. *European Journal of Personality, 22*, 427-455.
- Uher, J., & Asendorpf, J. B. (2008). Personality assessment in the great apes: Comparing ecologically valid behavior measures, behavior ratings, and adjective ratings. *Journal of Research in Personality, 42*, 821-838.
- Weiss, A., Inoue-Murayama, M., Hong, K. W., Inoue, E., Usono, T., Ochiai, T., Matsuzawa, T., Hirata, S., & King, J. E. (2009). Assessing chimpanzee personality and subjective well-being in Japan. *American Journal of Primatology, 71*(2), 283-292.
- Weiss, A., King, J. E., & Figueredo, A. J. (2000). The heritability of personality factors in chimpanzees (*Pan troglodytes*). *Behavior Genetics, 30*(3), 213-221.
- Weiss, A., King, J. E., & Perkins, L. (2006). Personality and subjective well-being in orangutans (*Pongo pygmaeus* and *Pongo abelii*). *Journal of Personality and Social Psychology, 90*(3), 501-511.
- Weiss, A., King, J. E., & Hopkins, W. D. (2007). A cross-setting study of chimpanzee (*Pan troglodytes*) personality structure and development: zoological parks and Yerkes National Primate Research Center. *American Journal of Primatology, 69*, 1264-1277.
- Yerkes, R. M. (1939). The life history and personality of the chimpanzee. *The American Naturalist, 73*(745), 97-112.